**Anatomy.** — *Notes on the telencephalon of Mormyrus and Gnathonemus.* By JEAN K. WESTON, Ann Arbor, Michigan [1]). (From the Central Institute for Brain Research, Amsterdam.) (Communicated by Prof. C. U. ARIËNS KAPPERS.)

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*Introduction.* In studying teleostean acousticolateral and cerebellar systems, particular interest centered on the brains of Mormyrus and Gnathonemus, where these systems are highly developed. The tracing of cerebellar fibers rostralward demanded a more exact knowledge of telencephalic and diencephalic structures. Certain of the former appeared distinctly different from those of other teleostean brains and worth recording. No attempt is made here to present a detailed telencephalic study, the available material imposing definite limitations, but the chief structural differences which Mormyrus and Gnathonemus exhibit from those of other teleosts (see GOLDSTEIN, '05; ARIËNS KAPPERS, '06; JOHNSTON, '11; SHELDON, '12; HOLMGREN, '20; and others) will be noted. The terminology used will be largely that found in ARIËNS KAPPERS, HUBER and CROSBY ('36), figures 544 and 545, in the text of which the homologies of these terms are clearly and specifically elucidated.

*Material.* The material available in the collection of the Central Institute for Brain Research, at Amsterdam, comprised: One transverse series of Mormyrus caschive with alternate sections stained after VAN GIESON and WEIGERT—PAL (counterstained with paracarmine); one sagittal series of Mormyrus caschive treated as the latter; one similarly stained transverse series each of Gnathonemus elephas, G. petersi and G. monteiri; ten whole brains of various Mormyroid fishes. The rich collection of other teleost brains possessed by the Institute [2]) was freely consulted.

*Olfactory bulb.* In Mormyrus, the olfactory bulb is small and lies close to the rostral pole of the telencephalon. Only a very small, unpaired, slit-like olfactory ventricle is demonstrable (fig. 1G, H). In Gnathonemus, the olfactory bulb lies farther from the telencephalon, and an unpaired, collapsed olfactory ventricle exists caudally, which bifurcates rostrally

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[1]) This study was in part completed while the author was on leave for one year from the Laboratory of Comparative Neurology of the University of Michigan to the Anatomical Institute of the State University of Groningen, Holland.

[2]) I am deeply indebted to Professor C. U. ARIËNS KAPPERS both for placing the resources of the Institute at my disposal and for his kind and helpful interest, to Professor ELIZABETH C. CROSBY for valuable criticisms and suggestions, and to Professor H. M. DE BURLET for the use of his technical staff and equipment, in the preparation of this communication.

into paired olfactory ventricles that fade out at the caudal ends of their respective olfactory bulbs. Both lateral and medial olfactory tracts are present. The former originates from the medial (and dorsal) portion, and the latter from the lateral (and ventral) portion of the olfactory bulb (fig. 1). This is interesting since most workers (SHELDON, '12, fig. 6; HOLMGREN, '20, fig. 30a) consider the reverse to be the case. Lack of silver or Golgi material made it impossible to pursue this matter more fully; similarly, the course of the nervus terminalis was inevident. The material confirms, so far as it goes, SHELDON's ('12) results relative to the distribution of the medial and lateral olfactory tracts.

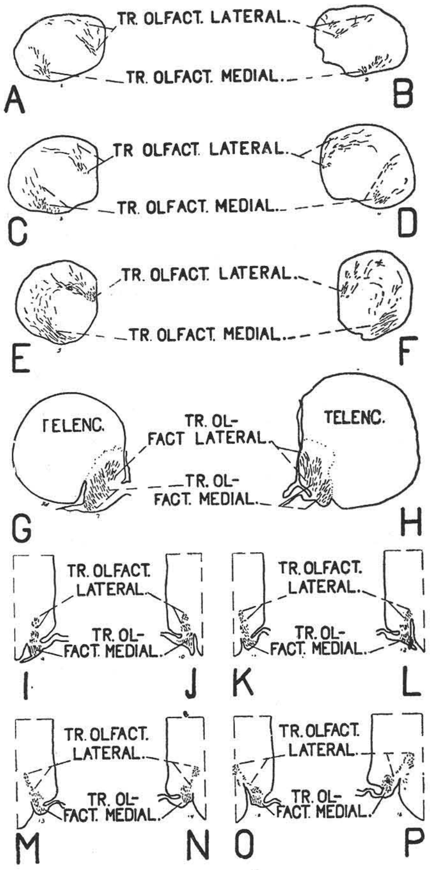

Fig. 1. Transverse hemisections through the olfactory bulb and telencephalon to illustrate the medial and lateral olfactory tracts in Mormyrus caschive. The hemisections on the left are the odd numbers, beginning with 1, and those on the right the even numbers, beginning with 2, of the series, consisting of alternate sections of one brain. The course of these tracts can be carried on in figure 2 I. WEIGERT-PAL preparations. × 15 (approximately).

*Nuclei.* The structure most characteristic of the Mormyroid telencephalon is the obvious nuclear mass at its ventrolateral surface (figs. 2, 3, 4). This is apparent grossly in Mormyrus as an elongated, oval elevation, bounded laterally by a shallow sulcus (deeper in Gnathonemus). It extends through about the middle third of the telencephalon, largely rostral to the anterior commissure. We will here be chiefly concerned with the description and interpretation of this mass.

Microscopically, this elevation consists of two distinct parts, provisionally designated as nucleus *a* and nucleus *b*. The nucleus *a*, composed of closely-packed, small, granule cells, is superficial throughout (figs. 2, 3, 4), excepting caudally, where it lies somewhat deeper (fig. 2B, F); in Gnathonemus its lateral portion is similarly withdrawn from the surface (fig. 3A). The nucleus *a* extends neither so far rostralward, lateralward, nor caudalward as does the nucleus *b*, which latter separates it almost entirely from other telencephalic structures. Medially (and caudally) the nucleus *a* abuts on the triangular shaped (in cross sections) area (*c*, figs.

2, 3) just lateral to the fissura endorhinalis; laterally and caudally it borders on the pars lateralis, area olfactoria dorsalis of Herrick. This

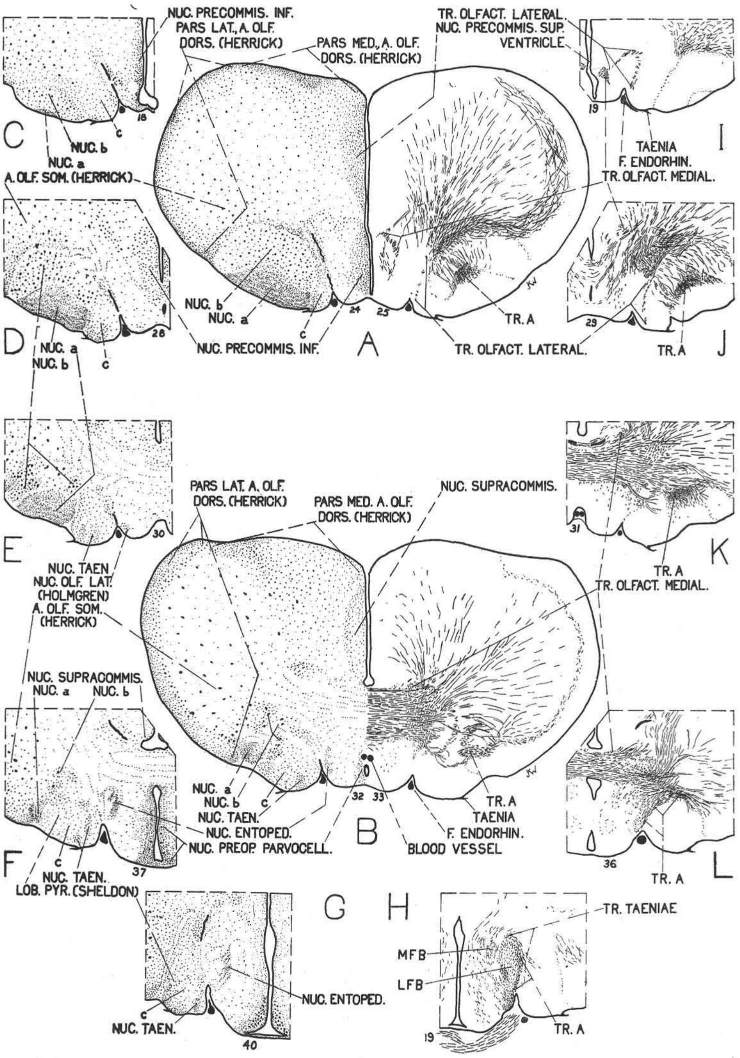

Fig. 2. Transverse hemisections and segments of such sections through the telencephalon of Mormyrus caschive to show the relations of the nuclei *a* and *b* and their fiber connections. Only those labels not obvious will be listed. The taeniae were either actually seen or were indicated where the change in epithelial structure from that lining the ventricle to that covering the surface of the brain was observed. A.OLF.SOM. (HERRICK), area olfactosomatica of HERRICK; F. ENDORHIN., fissura endorhinalis; LOB. PYR. (SHELDON), lobus pyriformis of SHELDON; NUC. ENTOPED., nucleus entopeduncularis (of SHELDON); NUC. TAEN., nucleus taeniae (of SHELDON). The left side of the figure was taken from the VAN GIESON series of alternate sections and the right side from the WEIGERT-PAL series; the numbers below indicate the number of the section in its respective series. × 18 (approximately).

nucleus *a* is always, excepting most caudally (where it consists of irregular cell groups; fig. 2B, E, F), sharply delimited dorsally from the nucleus *b* (not so sharply in Gnathonemus, fig. 3), due to their marked difference in cell type, as well as to the fibers and blood vessels which intervene. At first glance the cells of the nucleus *a* appear to fuse medially with the granule cells marking the taenia (fig. 2A, D, E), but close inspection shows no real continuity (see particularly Gnathonemus; fig. 3A). Here it should be noted that, in Mormyrus, the area *c* (fig. 2; see above) obviously passes over rostrally into the area lying lateral to the nuclei *a* and *b* (fig. 2A, C), which latter area it resembles very closely in cell type and distribution; a similar tendency is apparent caudally (see especially Gnathonemus elephas; fig. 3B). STENDELL ('14) figured this nucleus *a* in Mormyropsis anguilloides and labeled it as the lobus parolfactorius.

Lying dorsal to the nucleus *a*, and separating it throughout (excepting far caudally, and, in Gnathonemus, dorsolaterally as well) from other

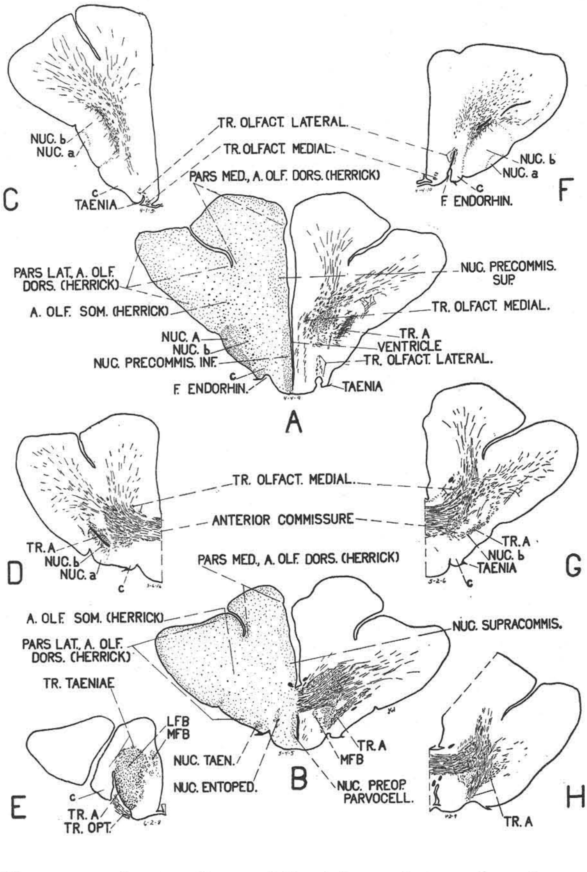

Fig. 3. Transverse hemisections of the telencephalon of various species of Gnathonemus: A, B, C, G, and E, Gnathonemus elephas; D, F, and H, Gnathonemus petersi. The taeniae were located as explained for figure 1. See fig. 1 for those labels not perfectly obvious. WEIGERT-PAL preparation. × 6 (approximately).

telencephalic structures, is a lighter-staining, sausage-shaped (in cross section) mass, consisting of numerous, very large, multipolar neurons. This is the nucleus *b*. It is marked off from the nucleus *a* as noted previously. A fiber net separates it dorsally (especially laterally) from the remainder of the telencephalon. Its relations are obvious in figures 2 and 3 (note its smaller size in Gnathonemus). STENDELL ('14) appeared not to have definitely differentiated this mass at all.

No similar structures seem to have been recorded in the literature, excepting for the work of STENDELL ('14). Neither were they demonstrable in any of the other teleostean brains in the collection of the Institute.

Two main connections characterize the nucleus *a* in the material available. One (the less heavily medullated) passes into the middle portion of the anterior commissure (fig. 2B, K), although its proportional derivation from the nucleus *b* and the telencephalic area immediately lateral thereto is not clear. Its further course is uncertain, although many of its fibers are apparently both decussating and commissural to contralateral telencephalic centers, while others obviously turn caudalward, after crossing, into the lateral forebrain bundle. This seems to be in part the homologue of the tractus bulbo-parolfactorius of STENDELL ('14, p. 33), which he believed might reach the medulla oblongata. The other is a strongly developed, predominantly uncrossed, heavily medullated one (tractus A, figs. 2, 3), definitely associated very largely with the nucleus *a* in Mormyrus. In Gnathonemus, due to the smaller sizes of the nuclei *a* and *b* and because the tractus A runs through the nucleus *b*, rather than between that mass and the nucleus *a*, this tract becomes more mixed with the fibers overlying the nucleus *b* (fig. 3A). The position of the tractus A in the lateral forebrain bundle is obvious and its course caudalward is unquestionable (figs. 2, 3, 4), although its exact distribution could not be ascertained. It apparently occupies the area in the lateral forebrain bundle assigned by SHELDON ('12, fig. 69) to the tractus strio-thalamicus incruciatus, but, being much larger than that tract as illustrated in his figures of the carp, it also occupies a large part of the area SHELDON labeled tractus strio-thalamicus cruciatus. It seems homologous, at least in part, with the tractus pallii of JOHNSTON ('11) and the tractus strio-thalamicus lateralis of HOLMGREN ('20). Although a portion of this tract definitely passes into the hypothalamic region (fig. 4), its exact distribution there is not clear. Another portion can be followed into relation with the nucleus rotundus and prerotundus, as SHELDON ('12) noted for the tractus strio-thalamicus, but here again, the terminal relationships are inconclusive. Further homolateral connections of the nucleus *a* with the other more lateral forebrain areas, but particularly with the nucleus *b*, appear likely from the material, but cannot be clearly differentiated. Neither is it possible to state definitely the direction of conduction in any of these tracts. This tractus A appears to be the homologue of the tractus taeniae of STENDELL ('14, see his figs. 18, 19, 21), but it must be emphasized that no part of the tractus A can be traced into the habenula (which STENDELL considered to be the termination of his tractus taeniae) in any of the material consulted (vide infra).

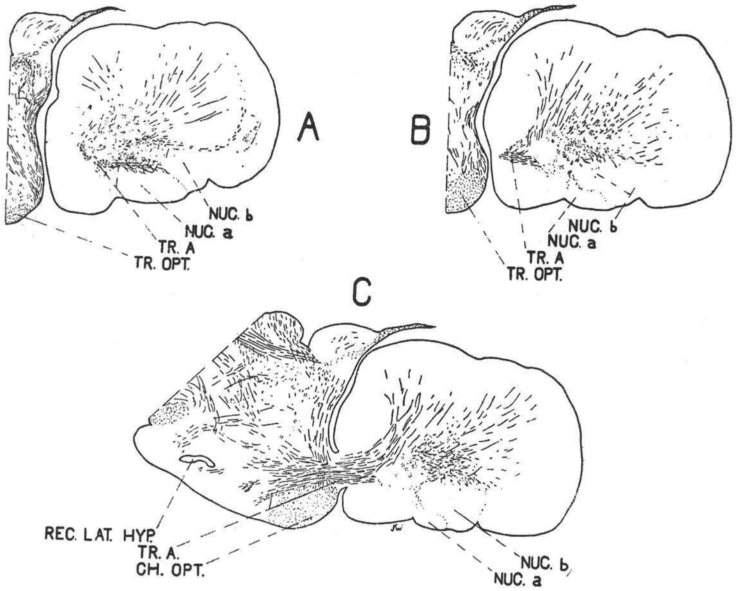

Fig. 4. Longitudinal sections through the forebrain of Mormyrus caschive, to illustrate the course of the tractus A. REC.LAT.HYP., recessus lateralis hypothalami. WEIGERT-PAL (5 ×, approximately).

The nucleus *b* contributes fibers which pass chiefly towards the anterior commissure (fig. 2); whether they be decussating, commissural, or both, is not clear. Connections with the nucleus *a* and with other homolateral forebrain centers seem obvious. An especially well-marked, rather heavily medullated connection from the more mediocaudal part of this nucleus *b* (fig. 2B, K), seemingly truly commissural, is in part homologous to the tractus bulbo-parolfactorius illustrated by STENDELL ('14, fig. 1).

No connection to either the nuclei *a* or *b* could be definitely established from either the lateral or the medial olfactory tracts. Should such connections be present they must be extraordinarily small.

The connections of the above-delineated area *c* (figs. 2, 3) deserve some mention. Fibers of the lateral olfactory tract obviously become lost throughout much of the area *c*. No interconnections between the area *c* and the nucleus *a* could be established, or (though less definitely) with the nucleus *b*. The area *c* contributes a few scattered fibers to the anterior commissure (fig. 2K). Its main connection, however, is a typical tractus taeniae of SHELDON ('12). This tractus taeniae is very small and consists chiefly of medullated fibers (figs. 2H, 3E). It originates in the area *c*, mostly caudal to the level of the anterior commissure, from two fairly obvious nuclei, which, because of these connections as well as their other relations (figs. 2B, E, F, G, 3B), seem entirely homologous to the nucleus taeniae and lobus pyriformis as illustrated and described by SHELDON ('12, carp) and illustrated by ARIËNS KAPPERS, HUBER and CROSBY ('36, sunfish). (HOLMGREN's, '20, figure 15, illustrated a nucleus taeniae in a similar position for Osmerus). This tractus taeniae could be followed caudally into relation with the homolateral habenular nuclei and into the habenular commissure. These facts adequately contradict STENDELL's ('14) identification of the nucleus *a* of this account as a strongly developed lobus parolfactorius, since on page 33 he said: "Der Name Nucleus taeniae ist ja ein Synonym mit Lobus parolfactorius......" However, in comparing this mass with the nucleus taeniae of the literature, he noted (p. 32) that "hier der Kern (his lobus parolfactorius) sich weit vor die Kommissure hinzicht, ja sogar mit dem grösseren Anteil vor ihr gelegen ist. Hierfür kann aber wohl die starke Entwicklung des Kernes der Grund sein".

The area lying lateral and dorsal to the nuclei *a* and *b* chiefly contributes fibers to the anterior commissure, although connections with the nucleus *b*, particularly, but to some extent with the nucleus *a*, seem indicated. There is some tendency for uncrossed fascicles from this area (fig. 2B) to accompany the numerous uncrossed fibers coming from the dorsomedial area of the telencephalon, which lie, in the lateral forebrain bundle, internal (and, more caudally, dorsal) to the tractus A.

## *Discussion and conclusions.*

Three reasonably possible explanations might account for the presence of the nuclei *a* and *b*. The *first*, that they are entirely new structures, has little in its favor. The *relative* hypertrophy of lateral line and cerebellar systems is the chief characteristic distinguishing the Mormyroid nervous system from that of the other teleosts. In view of this, and when we note their but mediocre optic and gustatory development (BERKELBACH VAN DER SPRENKEL, '15) and the reduced olfactory system, it would be most phenomenal to find two new structures only in the telencephalon, since almost invariably the appearance of a new structure in one part of the nervous system is correlated with the appearance of new structures elsewhere in that system. STENDELL ('14) related the development of his lobus parolfactorius (nucleus *a*) to the long snout of these forms, and considered the lateral line hypertrophy the result "eines noch unbekannten Oralsinns, der hier ausser vom Trigeminus wohl durch den Kopfast des Lateralnerven bedient wird". He subsequently ('14a) demonstrated special lip organs which he believed were related to lateral line organs and found them to be supplied by the anterior lateral line nerve. Since it is the posterior lateral line nerve and lobe that are most developed (see BERKELBACH VAN DER SPRENKEL, '15; SUZUKI, '32), it is difficult to believe the long snout responsible either for their development, or, in the apparent absence of other related specialized centers, for that of the nucleus *a*.

A *second* possibility is that these two nuclei are specialized ventrolateral portions of the telencephalon. This is in part STENDELL's ('14) interpretation, since he homologized the nucleus *a* with the nucleus taeniae. Valid reasons were given above for discarding this suggestion, as well as the possibility of their being an hypertrophied lobus pyriformis of SHELDON ('12). Another serious objection is the inevidence, in other teleosts with large lateral line and cerebellar systems, of any similar ventrolateral differentiations. This possibility may not be completely disregarded, however, for those ventrolateral telencephalic portions lying lateral to the lobus pyriformis of SHELDON ('12).

The *third* possibility is that we have here structures, better developed than usual, which are present in unusual surroundings, hence confounding any immediate homology with those of other teleosts. Certainly the above objections would seem to favor this notion; at least it is worth pursuing farther.

HOLMGREN ('20) noted for Osmerus that the large, centrally-lying cells of the area olfacto-somatica of HERRICK tended to be most densely grouped close inside the superficial portion of the telencephalon which HERRICK called the pars dorsalis, area olfactoria dorsalis (HOLMGREN's primordium pallii, pars dorsolateralis); in fact, his tendency was to consider both these areas as one mass. In comparing Mormyrus and Gnathonemus with other teleosts, this observation was repeatedly verified. It is further notable that the pars dorsalis, area olfactoria dorsalis varies considerably in size and position in different teleosts, and that the area olfacto-somatica shows concomitant changes in size and position. When, finally, the former area demonstrates an uncrossed, heavily medullated connection to the lateral portion of the lateral forebrain bundle, the size of which seems to vary with the size of that area and is otherwise suggestive of the tractus A, the obvious correlation could no longer be denied. Figure 5 demonstrates diagrammatically some of these relationships for several teleosts. No pars dorsalis, area olfactoria dorsalis occupies its usual position in Mormyrus (fig. 2); in Gnathonemus a deep fissure occurs in its stead (fig. 3). In both these forms there is but one place where a differentiable area of the massive telencephalic wall, bordering on the ventricle, can be found in close relation to the area olfacto-somatica of HERRICK, and that is ventrally and laterally (fig. 5A, L; compare figs. 2, 3).

Consequently, based in part on the relations to other telencephalic centers and in part on the fiber connections, it is concluded: (1) that the nucleus *a* is the exceptionally well-developed homologue of the pars dorsalis, area olfactoria dorsalis of HERRICK; (2) that the nucleus *b* is homologous to the area olfacto-somatica of HERRICK; (3) that the area *c* is a part of the pars lateralis, area olfactoria dorsalis of HERRICK, which has become separated from its usual lateral relations by the incursion of the nucleus *a*.

Considered from this angle, the large comparative development here of the pars dorsalis, area olfactoria dorsalis of HERRICK offers support of HOLMGREN's conception of this area as general pallium, since in these forms olfactory, optic, and gustatory sensibility are not highly developed while the lateral line system patently is. Further, it is possible, in view of its cell type, to consider this area as receptive, in which case the tractus A is probably the chief pathway over which thalamic centers relay the somatic sensibility (here probably largely lateral line in type) to this area. If this should be true, its ventral position in these forms might be explainable as due to the operation of neurobiotactic phenomena

(ARIËNS KAPPERS, '06). Similarly, the close relation of the area olfacto-somatica, its more efferent cell type, and the fact that it migrates with the pars dorsalis, area olfactoria dorsalis of HERRICK, probably mean,

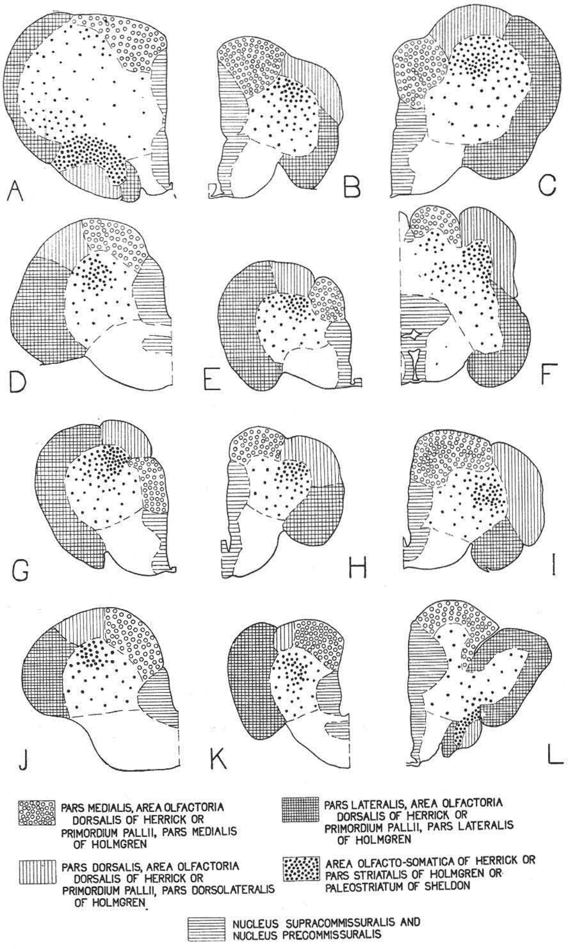

Fig. 5. Semi-diagrammatic transverse hemisections through the telencephalons of a variety of species of teleosts as listed below. The black dots indicate, in a general way, the relative density of distribution of the large cells characterizing the area olfacto-somatica of HERRICK. Note also the variation in size of the pars dorsalis, area olfactoria dorsalis of HERRICK, but keep in mind that apparent size alone in such a figure can give no true indication of the relative density of the small granule cells characterizing this area. A, Mormyrus caschive, × 11; B, Ophiocephalus striatus, × 8; C, Gadus aeglefinus, × 7; D, Carp, SHELDON's ('12) figure 38, page 273, copied; E, Lota lota, × 5; F, Monopterus javanensis, × 8; G, Motella mustela, × 8; I, Anguilla vulgaris, × 8; J, Osmerus eperlanus, HOLMGREN's ('20) figure 15, page 164, copied; K, Eupomotis gibbosus, ARIËNS KAPPERS, HUBER and CROSBY's ('36) figure 545A, page 1274, copied; L, Gnathonemus monteiri, × 8. WEIGERT-PAL preparations where not copied.

neurobiotactically considered, that it is chiefly concerned in discharging this latter area.

No valid explanation for the unusual (as compared with other teleosts) positions of these centers in Mormyrus and Gnathonemus can be offered. In addition to the neurobiotactic factors noted previously, pressure factors incident to the extreme cerebellar hypertrophy during embryologic development may be operative, since, among others, such factors undoubtedly play an important part in the development of the nervous system, especially in teleosts, as has been previously noted. In explaining the extreme *degree* of development of these nuclei, however (provided they have been correctly identified), it is not necessary to postulate a special 'Oralsinn' in the sense of STENDELL ('14), since we are dealing with a form possessing no great optic, gustatory or olfactory development, but an extreme development of somatic lateral line sensibility. Hence, if such somatic sensibility is projected via the acousticolateral lemniscus (as WALLENBERG, '07, in particular, believed), which here is very large, directly (or even indirectly by way of the tectum) onto the thalamus and from there onto the telencephalon, which seems entirely possible since they are interconnected, then the telencephalic area upon which it impinges should reflect to some noticeable extent any considerable variation in the development of such sensibility over the usual condition, particularly if other sensory centers are not highly developed to confuse the issue. These relationships might be adduced as indirect evidence of a sort in support of the previous conclusions.

The possibility of the nuclei *a* and *b*, together with the area *c*, being a primordial amygdaloid complex (which had not occurred to me and was called to my attention by Professor CROSBY) should also be noted. The position of these centers lateral and dorsolateral to the fissura endorhinalis is suggestive of such a relationship — more so are their connections. In mammals the lateral and basal amygdaloid nuclei (in most forms at least) do not receive olfactory tract fibers, composing, then, a somatic portion of the amygdaloid complex. Their other connections include commissural and crossed septal, preoptic, and hypothalamic fibers, as well as uncrossed amygdalo-hypothalamic and preoptic fibers running in part on the ventral (or ventrolateral) border of the lateral forebrain bundle. Certainly the connections of the nuclei *a* and *b*, so far as they could be unravelled in the material, are quite closely comparable. It is interesting, too, to note that in reptiles the somatic portion of the amygdaloid complex originates from the dorsal ventricular ridge, the homologue of which would probably be included, in fishes, in the pars dorsalis, area olfactoria dorsalis of HERRICK. The nucleus taeniae, with its olfactory tract and habenular connections, would homologize well with the mammalian medial amygdaloid nucleus, which receives olfactory tract fibers and connects with the habenula by way of a cortico- or amygdalo-habenular tract. The remainder of the area *c* would then correspond to the intermediate portions of the mammalian complex (i.e., those lying between the basal and lateral amygdaloid nuclei, on the one hand, and the medial amygdaloid nucleus on the other), which in part receive olfactory tract fibers and contribute a small connection to the anterior commissure.

The exact relation of the above observations to the notions of telencephalic development expounded by GAGE ('93), STUDNIÇKA ('95), ARIËNS KAPPERS ('06), JOHNSTON ('06), SHELDON ('12), and others, is not clear, but certainly they strongly suggest, if correct, that factors other than simple eversion or modified eversion are operative in teleostean telencephalic development. What is here most forcibly brought out, however, is the fundamental similarity of pattern of the teleostean telencephalon.

## *Summary.*

1. The olfactory bulbs of Mormyrus and Gnathonemus are small, with the lateral olfactory tract originating from their medial, and the medial olfactory tract from their lateral portions.

2. Two unusual ventrolaterally-lying nuclei are described. On the basis of comparative anatomic relations and fiber connections the nucleus *a* is homologized to the pars dorsalis, area olfactoria dorsalis of HERRICK, and the nucleus *b* to the area olfacto-somatica of HERRICK.

3. The area *c*, lying between the above two nuclei and the fissura endorhinalis is considered to be merely a displaced portion of the pars lateralis, area olfactoria dorsalis of HERRICK.

4. The possibility of these three masses being a primordial amygdaloid complex is considered.

## BIBLIOGRAPHY.

(Any references listed in the text and not found below can be obtained at the end of Chapters VIII or IX in the first reference listed below.)

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