The cytoarchitecture of the telencephalon of *Labroides dimidiatus* (Labridae).

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Abstract

As evidence for advanced cognitive abilities in fishes steadily increases, cytoarchitectonic studies of the Actinopterygian telencephalon receive increasing interest by neuro-ethologists. However, the amount of information concerning brain organization in this group is still rather small. Here, we present a cytoarchitectonic analysis of the telencephalon of *Labroides dimidiatus*, a species showing highly sophisticated interspecific social behavior in cleaning interactions with other reef fish species. Analysing cresyl violet-stained serial transverse sections, we designated cell regions and nuclei on the basis of characteristic size, shape and intensity of pericarion staining, density and distribution of cell bodies, cell-poor zones; congruence of cell groups with brain cellular structure identified in other species, consistent sequence of cell groups in subsequent sections and in corresponding centres of the opposite hemisphere. 27 telencephalic regions and nuclei, 9 in the ventral part and 18 in the dorsal part of the telencephalon were recognized and described.

Keywords: Labroides dimidiatus, Telencephalon, cytoarchitecture, animal cognition

Introduction

There is increasing interest in the cognitive abilities of fishes, especially of ray-finned bony fish (Actinopterygii) (Brown et al. 2011; Bshary et al. 2014; Brown 2015; Luton-Xiccato et al. 2017; Bshary and Triki 2022). There are several reasons for this interest. First, ray-finned fishes have been shown to possess a great variety of cognitive tools that go beyond basic associative learning (operant and classical conditioning). There is experimental evidence for cognitive maps in rock-pool blennies (Aronson 1971), transitive inference (Grosenick et al. 2007), complex social learning rules (Laland 2004, Hoppitt and Laland 2013), referential gestures (Vail et al. 2013), generalization (Wismer et al. 2016) or mirror self-recognition (Kohda et al. 2019, 2022, 2023). Second, fish live in highly diverse habitats and may differ greatly with respect to social organization. Most famously, cichlid fishes show a great variety of social systems (Jungwirth and Taborsky 2015, Taborsky 2013). Such diversity offers great opportunities to study associated variation in social behavior (Jordan et al. 2021; Lein and Jordan 2021), physiological changes in the brain (Fernald 2015, 2016, Loveland and Fernald 2017), and eventually variation in cognitive performance. Third, comparative research on vertebrate brains has identified amazingly conserved structures with respect to a so-called social decision-making network, which consists of the ‘social behaviour network’ and the ‘basal forebrain reward system’ (O’Connell and Hofmann, 2011, 2012). The mesolimbicreward system and the social behavior network comprise 13 brain regions that are interconnected and are present in all vertebrates (O’Connell and Hofmann, 2011). Most parts of the mesolimbic reward system are situated in the telencephalon, regions Dm, Dl, Vd, Vc the homologues of basolateral amygdala, hippocampus, nucleus accumbens and striatum respectively, with functional connection between those two systems situated in medial amygdala and lateral septum, the Vs and Vl/Vv nuclei in fish (O’Connell and Hoffmann, 2012). Given these similarities, fishes seem to offer vast opportunities for testing general principles concerning social behavior and underlying cognitive mechanisms and processes (Brown et al. 2011; Bshary et al. 2014).

While there are many similarities between ray-finned fishes and endotherm vertebrates (mammals and birds) with respect to behavior, cognitive processes and parts of brain organization, there are also very important known differences. First, the average ray-finned fish brain relative to body weight is about ten times smaller than in the average endotherm (Jerison 1971; Tsuboi et al. 2018). This huge difference raises the question what endotherms can do that Teleostei fish cannot. Second, there seem to be major differences in brain organization. For example, intraspecific brain-body slopes are very different between mammals and fishes, with the former yielding estimated slopes of 0.25-0.3 (van Schaik et al. 2021) and the latter slopes of about 0.45, albeit with large between-species variation (Triki et al. 2021). Furthermore, it is well known that the ray-finned fish telencephalon undergoes a process called eversion versus evagination in tetrapods (Butler and Hodos, 2005). As a result of eversion during development, the topology of the telencephalic pallium is transverse compared to Tetrapods (Broglio et al. 2005; Holmes and Northcutt, 2003; Yamamoto et al. 2007).

Currently, aims to link inter- and intraspecific variation in ecology and cognitive performance to variation in underlying brain structures (as well as physiological processes in these structures) are limited by a lack of detailed knowledge regarding brain regions. Such knowledge requires detailed brain atlases for a variety of species of interest, so that comparative research can go beyond correlating ecology and cognitive performance with overall brain measures and/or major brain areas like the telencephalon. Arguably, the textbook example about what insights can be gained from a focus on more specific brain regions involves between and within species variation in spatial memory and the hippocampus. Variation in hippocampus size predicts for example spatial memory performance i) across bird species that rely to different degrees on food caching (Krebs et al. 1989; Sherry et al. 1989), ii) between bird populations of the same species that rely to different degrees on food caching (Pravosudov & Clayton 2002), between female and male birds of the same species (Sherry et al. 1993), and iv) the ability of London taxi drivers to navigate the complex traffic network of the city (Maguire et al. 2006).

Here, we describe the basic cytoarchitecture of the telencephalon of the cleaner fish *Labroides dimidiatus*. This fish from the indopacific removes ectoparasites from visiting reef fish species, so-called clients (Côté 2000). It is of potential interest for more detailed brain research because it shows highly sophisticated social strategies and a variety of advanced cognitive processes (Bshary 2010). Regarding social strategies, it manipulates client decisions and reconciles with clients after a conflict (Bshary and Würth 2001), it uses predatory clients as social tools against aggressive non-predatory clients (Bshary et al. 2002), and it behaves more cooperatively towards a current client if observed by a bystander client (Pinto et al. 2011. Various studies show that cleaner outperform other fish species and even mammals, including primates, at learning tasks that are ecologically relevant to cleaning (Salwiczek et al. 2012; Gingins and Bshary 2016; Mazzei et al. 2019). Regarding the underlying cognitive processes, cleaners have been shown to use generalized rule learning (Wismer et al. 2016), high self-control as measured by their ability to delay gratification (Aellen et al. 2021), standard numbering competences (Triki & Bshary 2018), extensive long-term memory (Triki & Bshary 2019), the ability of mirror self-recognition based on a mental image of self (Kohda et al. 2019, 2022, 2023), the ability of sequential and configurational learning (Quiñones et al. 2020, Prat et al. 2022; Truskanov et al. 2021) as well as social learning of cleaning strategies (Truskanov et al. 2020). A potentially interesting negative result is that cleaners apparently lack the general intelligence factor ‘g’, as individual relative performance in one task did not predict its relative performance in other tasks (Aellen et al. 2022). Yet another interesting feature of cleaners is that their performance may vary in some tasks as a function of local intra- and interspecific fish densities (Wismer et al. 2014, 2018; Binning et al. 2017; Triki et al. 2018, 2019, 2020), as well as between males and females (Triki & Bshary 2022). While L. dimidiatus has an overall brain volume that is rather average for a wrasse of its size (Chojnacka et al. 2015), fish densities affect forebrain size and number of cells in their forebrain (Triki et al. 2019b, 2020). Hence, having a more detailed brain atlas may allow to eventually pinpoint the locations involved in the strategic sophistication, the various cognitive processes as well as a more detailed understanding on the variation in major brain areas.

The focus on the telencephalon can be justified not just by the data showing its variable size in cleaners (Triki et al. 2019, 2020) but more importantly by the accumulating evidence of its key role for more advanced cognitive processes in fishes. Already classic ablation studies showed that the telencephalon is key for coordinating different behaviours in a meaningful sequence, like nest building (Schönherr 1954, Seegar 1956; Lopez et al 2000; Portavella et al. 2002). More recently, selection on telencephalon size in guppies revealed its eminent role for so-called executive functions, i.e. top-down control mechanisms like flexibility, self-control and working memory (Burkart et al. 2016). Guppies with enlarged telencephalon outperformed down-selected guppies in tasks testing for executive functions, like reversal learning, detouring to reach a food source, and object permanence (Triki et al. 2022a, 2022b, 2023). A description of the basic cytoarchitecture of telencephalon of *Labroides dimidiatus* can hence be a useful base for the precise localization of the neuroendocrine territories and for the tracing of the neuronal connections, investigation of types and distribution of neurons in each centre, hormone concentration and gene expression and comparative research of regions potentially engaged in control of cognitive behavior. Basic neuroanatomical data will allow the study of the functions of each nucleus in the brain of this species and other related perciform fishes, in particular closely related species in the family Labridae with different degrees of behavioural complexity.

Materials and methods

Adult individuals used in the study were obtained from an importer of aquarium fish, and therefore their exact origin is unknown. We used both fish that for various causes did not survive transport or acclimatization, and live individuals, according to permit no. 70/05 from the Local Ethical Committee for Experiments on Animals. Individuals intended for the study were euthanized with MS222, dose over 250mg/l of water. Because

MS222 is a low-pH agent, its solution was buffered with sodium hydroxide to prevent shock in fish transferred to it (Welker et. al 2007).

Before brain dissection, all fish were measured for morphometric features, i.e. body length and weight. The brain was dissected from the spinal cord at the level of the first spinal nerves and weighed after the removal of cerebro-spinal meninges and blood vessels.

Dissection

Individuals were collected from a pet shop, where they had died of unknown causes. Shop staff put whole individuals in 75% rubbing ethanol for preservation not later than 24 hours after death, before we picked them up. The individuals were additionally preserved for 10 days in 6% buffered formalin.

After dissection brains were washed in tap water for 24hrs, dehydrated in a series of alcohol solutions (30% - 1h, 50% - 2h, 70% - at least 2h, 90% - 2h, 96% - 2h, 100% - 4h, 100% - 4h), then washed in xylene for few seconds, and embedded in paraplast.

For microscopic analysis 7μm-thick serial transverse sections were cut on a Leica RM rotary microtome. Sections were applied on microscope slides and stained with cresyl violet (Nissl method). The protocol followed was a slightly modified method which is popular for these types of studies, and has been described many times in relevant literature (Davenport, 1960; McNally and Peters, 1998). Individual protocol steps include: immersion in a series of hydrating dilutions of xylene and alcohol (xylene - 3 times for 5min, alcohol: 100% - 3min., 100% - 3min., 96% - 2min., 80% - 2min., 70% - 2min., 50% - 2min.), and a final wash in distilled water for 1min. Sections were then stained with 2% cresyl violet solution (100ml water and 2g solid cresyl violet) for 2min and washed in differentiating solution (acetic aldehyde: 100ml 100% alcohol and 2μl of concentrated acetic acid). Cresyl violet stain differentiates nervous tissue. Sections were then dehydrated in a series of alcohol solutions (90%, 96%, 100%) for 2 minutes each, xylene (2 x 3 minutes) and mounted in DPX resin.

Different groups of cells were identified based on the following criteria:

1. Characteristic size, shape and intensity of pericarion staining
2. Density and distribution of cell bodies
3. Cell-poor zones;
4. Intensity of background (neuropil) staining
5. Relationship of cell groups to the anterior commissure and external sulci.
6. Congruence of cell groups with brain cellular structure identified in other species.
7. Consistent sequence of cell groups in subsequent sections and in corresponding centres of the opposite hemisphere.

Brain sections were preliminarily analyzed under a Nikon Eclipse 80i microscope and photographed at different magnifications with a Nikon Coolpix 4500 camera, and further scanned under an Olympus BX51 microscope for more detailed analysis. Images were saved in a digital format and analyzed with the dotSlide virtual microscopy system and OlyVIA image viewer software from Olympus Soft Imaging Solutions GmbH 2008. For the images of selected representative sections diagrams were added, with identified and described morphology regions. Representative sections were chosen, at 50, 100 or 130μm intervals. The slides and diagrams are available on http://blackfishone.net/publications/pub2023-237/.

Where possible, we used the nomenclature of Northcutt (2006) which is a modification of the nomenclature used by Northcutt and Braford (1980) (Tab. 1).

Results

Our main aim is to present the cytoarchitectonic of the telencephalon of *L. dimidiatus*. As the majority of cell groups which compose telencephalon in Actinopterygii were precisely studied and described in a few species, we summarise those results in Tab. 2 to facilitate a comparison. Furthermore, these species are plotted on a phylogenetic tree so that the currently existing information on fish telencephalon cytoarchitectonic structure can be viewed with an evolutionary perspective (Tab. 3). In general, the Actinopterygian telencephalon is composed of two olfactory bulbs (OB) situated anteriorly and ventrally to brain hemispheres and ventral (V) and dorsal part of telencephalon (D), the equivalents of subpallium and pallium of other vertebrates, (Butler 1992; Meek and Nieuwenhuys 1998; Nieuwenhuys and Pouwels 1982; Northcutt and Braford 1980; Reiner and Northcutt 1992; Wullimann and Rink 2002, Wullimann and Mueller 2004; Wullimann 2009; Mueller and Wullimann 2015). A consensus also exists on the identification of the posterior pallial zone (Dp) as the homolog of the olfactory cortex (Wullimann and Mueller 2004; Nieuwenhuys 2009). Comparative, neurohistochemist and behavioral research shows that the Actinopterygian dorsal telencephalon contain subdivisions homologous to amygdala, hippocampus and isocortex of tetrapodes, Dm, Dlv and Dld and Dd respectively (Broglio et al. 2003; Butler 1994; López et al. 2000; Rodriguez et al. 2002; Yamamoto et al. 2007; Mueller and Wullimann 2015). Moreover, a center of multimodal integration in the telencephalon is Dm (Prechtl et al. 1998; Yamane et al. 1996). In the text, we focus on the cytoarchitectonic structure of *L. dimidiatus*, detailed comparison of the number of nuclei and regions in the telencephalon is summarized in Tab. 2.

Olfactory bulbs

Olfactory bulbs (OB) terminate directly without secondary olfactory tracts and are thus sessile in this fish. OB of *Labroides dimidiatus* are very small compared to other teleosts and only two visible layers can be distinguished: a granular cell layer (GCL) situated in the dorsal-most part of the olfactory bulb and the glomerular layer (GL) with its less densely packed cells. Usually four concentric cell layers can be distinguished in other fish with OB situated rostrally to the telencephalon with only more caudal parts lying ventrally to the telencephalon (Karoubi et al. 2016, Baile and Patle 2011, D'Angelo 2013). OB in *Labroides* are so small that they can be distinguished only in a small part of the ventral telencephalon without protruding to the rostral part of telencephalon.

Telencephalic hemispheres

The telencephalic hemispheres can be divided into two main divisions, the ventral part (V; composed of nuclei) and dorsal part (D; composed of areas and regions). We recognized and described 27 telencephalic regions and nuclei, 9 in the ventral part and 18 in the dorsal part of the telencephalon. The total number is slightly larger than in studies on other fish species using the same methods (Baile and Patle 2011; Cerda-Reverter et al. 2001).

Ventral telencephalon

The ventral area presents a rather constant pattern among the actinopterygian fishes (Nieuwenhuys 1963; Northcutt 1995) as compared to the dorsal area. In the ventral telencephalon of *L. dimidiatus*, like in other actinopterygians, four main cell nuclei, dorsal (Vd), ventral (Vv), supracommissural (Vs), and postcommissural (Vp), were observed (D'Angelo 2013; Anken and Rahmann, 1994; Burmeister et al. 2009). Moreover, commissural (Vc), lateral (Vl) and entopeduncular (EN) nuclei, which tend to be more variable in their presence among teleosts, were recognized in the subpallium of *L. dimidiatus*.

The most rostral cell cluster of the ventral telencephalon is called the nucleus supracommissuralis (Vs). It consists of small, heavily stained and densely packed cells, which become more scattered in the caudal part. It originates near the ventricle as an oval compact nucleus, which extends into the dorsal direction remaining in the paraventricular location. It ventrally adjoins the Dm3 zone. It originates exactly at the boundary of the ventricle. The nucleus supracommissuralis is followed by the nucleus postcomissuralis (Vp) in the more caudal part of the ventral telencephalon (Fig. 2-4, 10, 11).

The dorsal nucleus of the ventral telencephalon (Vd) is composed of very small and very heavily stained cells grouped in tiny clusters. This region originates at the lateral side of the Vs area and extends in a crescent-like shape to the latero-dorsal direction (Fig. 2-4, 11,13).

The ventral nucleus of the ventral telencephalon (Vv) originates in the paraventricular area, ventrally to Vs and Vd, and extends towards the lateral and dorsal area. It is characterized by very small, heavily stained cells, grouped in clusters, which become dispersed and combine into groups to form a compact, sharply demarcated region. In the caudal direction the nucleus extends laterally and the cells become more loosely distributed and scattered. Caudally, the Vv area separates into two additional nuclei, Vv-m stays in periventricular position, Vv-l moves laterally (Fig. 3, 4, 10).

Vd, Vs and Vv in *L. dimidiatus* all starts rostrally in ventricular position caudally moving to more central part of telencephalon, which according to Butler and Hodos (2005) is one of the characteristics of a more derived and complex brain structure.

The nucleus postcomissuralis (Vp) is composed of very darkly stained cells, arranged in groups, which form very distinct columns parallel to the surface of the telencephalon. From the dorsal side it is bordered by Dm4, from the ventral side by Vv-m. It originates in periventricular position. Caudally, it merges with the Vv nucleus (Fig. 4-7, 12).

The nucleus commissuralis (Vc) is closely associated with the sulcus externus, composed of large cells that are grouped around the sulcus, intersected by nerve fibers running towards Dc. It originates as a set of medium-sized to large cells (especially in the caudal area), located dorsomedially to the sulcus externus. This small nucleus is composed of a few small cells in the rostral part which become larger and diffuse caudally. The spongy neuropil is traversed by blood vessels and nerve fibers (Fig. 4-6, 14, 15). The position associated with sulcus externus is also described in most studied species.

A very small lateral nucleus (Vl) (Fig. 5, 15) is located in the rostral part of telencephalon close to the ventral surface of the telencephalon, with not clearly delimited boundaries. It is composed of several medium-size to large cells.

The entopeduncular nucleus (EN) is the most variable structure of ventral telencephalon in ray-finned fish (Baile and Patle 2011). In *L. dimidiatus* it is composed of an intensely stained and very densely packed single cell population that extends into the diencephalon. As in other teleosts it is closely associated with the forebrain bundles (Fig. 7, 16).

Dorsal telencephalon

The dorsal telencephalon of ray-finned fish shows much more interspecific variations than the ventral telencephalon, due to differences in the eversion processes of the telencephalic walls, different hypertrophy and thickening of cerebral walls (Butler and Hodos, 2005). Nevertheless, in *L. dimidiatus*, as in other teleosts, the dorsal telencephalon can be divided into four main areas: the medial (Dm), dorsal (Dd), central (Dc) and lateral (Dl), where each can be subdivided into many distinct cell groups. The Dp could not be distinguished or is wrongly interpreted as Dlp in this species, and more precise studies of neuronal connections need to be carried out. The basis for this division is the relatively simple pallium of the zebrafish, in which basically undivided Dm, Dl, Dd, Dc and Dp are recognized (Wullimann, 1996).

The medial part (Dm) of the telencephalon in *L. dimidiatus* is divided into 4 main areas: Dm1, Dm2, Dm3 and Dm4. Dm is located in the rostrocaudal area, reaching the most caudal part of the dorsal telencephalon. The Dm regions are named sequentially in the order in which they appeared (Fig. 1-9, 12, 17-21).

The most rostrally located Dm1 region in *L. dimidiatus* is ventrally enclosed by the acellular zone separating it from Dc. Caudally it moves laterally from the paraventricular side. The cells are medium-sized, relatively pale and blurry. In the rostral part, the cells are grouped, while in the caudal part they become scattered, making it difficult to determine the boundaries of the caudal area of this region and two sub-regions with higher cell density, located parallel to the ventricle can be distinguished (Fig. 18). They originate in the paraventricular area as two subdivisions, Dm1d and Dm1v, and make extensions towards the central and dorsal parts, replacing or merging with the Dm1 region. The cytoarchitecture of Dm1d and Dm1v areas slightly differ. Dm1d contains medium-small, relatively darkly stained and densely packed cells. The cells appear blurred and stretched. The sub-region Dm1d is made up of very small, heavily stained and closely packed cells which are not aggregated, and it is located ventrally to Dm1d, extending from the edge towards the centre (Fig. 1-3, 17, 18).

Region Dm2 is composed of large and medium-sized cells, bordering laterally with Dld. Its cellular composition resembles the Dm2 area described by Burmeister et al. (2009) in *Astatotilapia* (*Haplochromisi) burtoni*. The cells of the rostral part of Dm2 are slightly larger than the Dm1 cells, but smaller than the cells of Dc. Dm2 originates rostrally, adjacent to Dld. Caudally, the cells are scattered, which makes the borders ill defined (Fig. 1, 2, 17). Because of its large cells, this region may be also considered as additional subdivision of Dc, associated with Dld or with an additional internal layer of the Dld.

Region Dm3 is composed of medium and small-sized, highly aggregated and heavily stained cells. In the caudal area the cells become more diffuse. This wide region covers dorsal and dorso-medial parts of the telencephalon. It is composed of cells aggregating in columns perpendicular to the surface of the brain, with columns being separated by cell sparse bands and differ slightly in cellular arrangement (Dm3d is composed of predominantly large and densely packed cells, Dm3v composed exclusively of small cells). Caudally, the layers merge into one area and extend towards the ventral side (Fig. 3-8, 19-21).

Region Dm4 arises dorsally to the paraventricular area. In the ventricular area it arises as a stripe of dark cells, extending centrally and dorsally. It is composed of very small darkly stained cells. This region is characterized by clear stratification. The cellular layers are arranged alternately with areas less densely packed with cells, and concentrically bordering an area composed of large cells, which can be classified as a Dc subregion due to the cell size (Fig. 4-9, 12, 20).

As the name implies, the central area (Dc) is usually located in the central zone of the dorsal telencephalon, between the medial, dorsal and lateral areas. In *L. dimidiatus,* however, it extends towards the dorsal surface of the pallium in the rostral part of the telencephalon. A similar deviating description was obtained by Karoubi et al. (2016) for the *Toxotes chatareus* pallium, where they stated that its commonly accepted central, large-celled part has a stalk-like continuation toward the everted ventricle, at least in the anterior telencephalon. The authors further classified this stalk as belonging to Dc. This can be correlated with the recently proposed claim that Dc should not to be confined to a centrally located pallial division as previously believed (Mueller et al. 2011). In other words, the central zone may be a histogenetic unit with its own ventricular zone and may correspond to the dorsal pallium (i.e., isocortex) (Karoubi et al. 2016). In the caudal telencephalon, the cells of Dc concentrate only in a central position, without protruding to the dorsal telencephalon. Dc in *L. dimidiatus* contains very large spindle-shaped, lightly stained cells with dark nuclei, which are widely scattered throughout the neuropil. In the caudal part of the area the cells are less abundant and more dispersed. As in other teleosts (Baile and Patle 2011, Munoz-Cueto et al. 2001), the central part is subdivided into at least two subregions: Dc1 and Dc2, where Dc1 is the largest subregion with several additional clusters of cells in its caudal part. Dc2 originates more rostrally and ventrally to Dc1. At the rostral side, Dc1 is separated from Dc2 by an acellular zone. Dc2 is laterally bordered with the Dld region, ventrally with Dlv1 and Dlv-pv, and it borders with Dc1 at the dorsal and intraventricular sides. It is composed of very large scattered cells, which are packed more densely at the edge. It joins the Dc1 more caudally. The neuropil of the Dc1 is light and spongy in structure, with numerous "holes" (Fig. 1-7, 22). Parvalbumin (Mueller et al. 2011) and calretinin (Castro et al. 2006) have been used in the zebrafish pallium to outline Dl/Dc versus Dm, respectively, and similar studies in *L. dimidiatus* with calcium- binding proteins may reveal more clearly the extent of pallial divisions such as Dc (Karoubi et al. 2016).

The dorsal area of the dorsal telencephalon (Dd) in *L. dimidiatus* is associated with the sulcus ypsiloniformis (Sy). The neuropil of Dd is very darkly stained, with small cells grouped in tiny clusters. In the rostral telencephalon, the nucleus is medially bordered with Dm3, from which it is separated by a virtually acellular structure. Laterally, it borders the dorsal part of the lateral telencephalon (Dld). At the caudal side, it becomes wider, forming an inverted triangle. As the central part of the dorsal telencephalon Dm3 increases, the nucleus slightly extends to the side, and finally it seems to combine with Dld (Fig. 4-7, 19, 23). A similar position and characteristics of cells is described in other perciform fishes (Northcutt and Davis 1983; Marino-Neto and Sabbatini 1988; Cerda- Reverter et al. 2001, D’angelo 2013, Baile and Patle 2011). Only Riedel (1997) described in the blind cave fish *Astuanax hubbsi*a a dorsal part formed by large cells. Dd is interpreted by Mueller et al (2015), as a part of the lateral pallial zone in *Danio rerio*.

The lateral area of the dorsal telencephalon (Dl) is one of the most expanded components of the wrasse’s telencephalon. It extends throughout the entire rostrocaudal part of the dorsolateral and ventrolateral regions in both brain hemispheres. The lateral area consists of 2 main regions: ventral (Dlv) and dorsal (Dld) (Fig. 1-8, 23-28).

The ventral region of Dl in *L. dimidiatus* is subdivided into three cell populations: Dlv1, Dlv-pv and Dlv-mg. In the rostral part, the boundary between the Dlv1 and Dlv-pv areas is clearly demarcated, and these regions differ with respect to cell size and density. Dlv-pv consists of small, tightly packed cells, resembling cells of the Dld region. Dlv-pv is located at the lateral side of the Dlv1 area, extending laterally to Dld, centrally overlapping Dlv-mg. Dlv1 cells are medium-sized to large, pale, slightly blurred, unevenly distributed and fairly densely packed. Dorsally Dlv1 is surrounded by an acellular zone. Some cells of the region are arranged in lines perpendicular to the ventral edge. Dlv1 is located more rostrally, bordering medially with Dc1 and caudolaterally with region Dlv-pv. Caudally, Dlv1 is changing position to the mid-ventral area, towards the ventricle. Dlv-mg cells are very large, resembling cells of the Dlv1 area. They possibly represent one structure separated by blood vessels (Fig. 1-5, 24, 27, 28).

The dorsal region of the lateral area of dorsal telencephalon (Dld) is poorly distinguishable from Dlv-pv as the lateral part of Dld is characterized by the same cell size and similarly stained neuropil, especially in caudal telencephalon. However, in the Dld area, a distinct cortical structure made of at least 4 layers is present. The layers differ in terms of cell size and distribution. Layer no. 1 is located in the dorsolateral part by the outer margin, and is formed by very small, moderately stained cells. Layer no. 2 is also formed by very small cells, but these are more intensely stained and more densely arranged than in other layers. Within this layer a single tract of cells is formed, which then transforms into the V-shaped region, caudally changing into a layer parallel to the lateral margin. Layer no. 3 is formed by very small cells (smaller than in layer no. 2) which are intensely stained, and caudally connects with other layers. Layer no. 4 is formed by very small, intensely stained and sparsely distributed cells. Caudally, the layers overlap and merge into a single area (Fig. 1-5, 24-26). According to Butler and Hodos (2005), a layered structure is one of the features characterizing more complex/developed brains.

The wrasse’s region Dlp is very poorly demarcated. It originates in the most caudal part of the telencephalon, composed of cells similar to cells of the Dlv-pv area, separated only by a blurred acellular zone. Caudally, it merges with Dlv-pv and Dld (Fig. 5-8, 23, 26). It may also constitute a part of Dlv/Dld region. Dp is considered a principal target of secondary olfactory fibers (Northcutt and Braford 1980). It is found in most studied species but in *L. dimidiatus*, the Dp could not be characterized probably due to the limited importance of olfaction in this species. Crucial for identifying with certainty the posterior pallial zone (Dp) will be to find connections to the olfactory bulb.

In the caudal telencephalon the nucleus taeniae (NT) can be distinguished situated on the border between subregion Dlv-pv and sulcus externus. It is composed of small, densely packed cells (Fig. 5-7, 28).

General discussion

Overall, the general cytoarchitectonic of the telencephalon of *L. dimidiatus* presents similar organizational patterns to those described for other acantomorphs teleost (Cerda-Reverter et al. 2001a; Pepels et al. 2002; Burmeister et al. 2009; D’Angelo, 2013, Karoubi et al. 2016, Baile and Patle 2011), although topographical arrangement and number of telencephalic cell masses exhibit variation in different species. The results raise the question to what extent the organization of the cleaners’ brain differs from that of closely related fish species that do not clean. More detailed analyses of the volumes of different nuclei and regions may eventually yield some hypotheses.

As it stands, Labridae are the most common family on coral reefs (Westneat and Alfaro, 2005). The family is large and diverse, with over 600 species in 82 genera. They are the second largest family of marine fish and one of the most diverse morphologically, behaviorally and ecologically. The diversity of family Labridae attracts considerable interest in scientists studying ecology and evolution of this group, life history and biomechanics, often linked to the evolution of cleaning behaviour (Clements et al. 2004; Ferreira et al. 2004; Rocha et al. 2004; Westneat and Alfaro, 2005; Baliga & Law 2016; Baliga & Mehta 2016).

One possibility is that brain structure does not differ much between closely related species but that receptor densities and gene expression patterns change according to ecological needs. Indeed, there is first evidence from transcriptomic analyses that there are specific gene networks associated with cleaning activity (Young et al. 2022; Kang et al. 2023). The former analysis was based on two telencephalic nodes of the Social Decision-Making Network, the medial (Dl; lateral part of the dorsal telencephalon) and the lateral pallium (area Dm; medial part of the dorsal telencephalon). The network is critical for evaluating stimulus salience and regulating sexual, aggressive, and parental behavior across vertebrates (Goodson 2004; O’Connell & Hofmann 2011, 2012). We sincerely hope that our atlas will help identifying such nodes as well as other telencephalic areas in wrasse for further comparisons. Furthermore, the atlas provides a starting point for explanations for the reported intraspecific variation in the behavior and cognitive performance of *L. dimidiatus* individuals (Wismer et al. 2014, 2018; Binning et al. 2017; Triki et al. 2018, 2019, 2020).

Future comparative research on the links between fish brain features and cognitive performance will depend on the availability of brain atlases, as well as a characterization of cell types, cell densities, receptors, and gene activity patterns. Thus, our telencephalon atlas for *L. dimidiatus* is just a first step, especially as recent research indicates that different major brain regions may be important for the cognitive performance in the same task depending on the species: for example, intraspecific variation in performance in reversal learning as a measure of cognitive flexibility and a detour task as a measure of self-control was correlated with telencephalon size in guppies and with the mesencephalon and cerebellum in cichlids *Neolamprologus pulcher* (Triki et al. 2023; Guadagno and Triki 2023). Nevertheless, given the similarities described above between the *L. dimidiatus* and other teleost fish, the atlas can be used with caution as a reference guide for investigators starting to work in other wrasse models. Apparently, a reference genome for *L. dimidiatus* is also about to be established (José Paula, pers comm). There is thus potential that *L. dimidiatus* becomes a model organism for highly integrative behavioural research on wrasse.

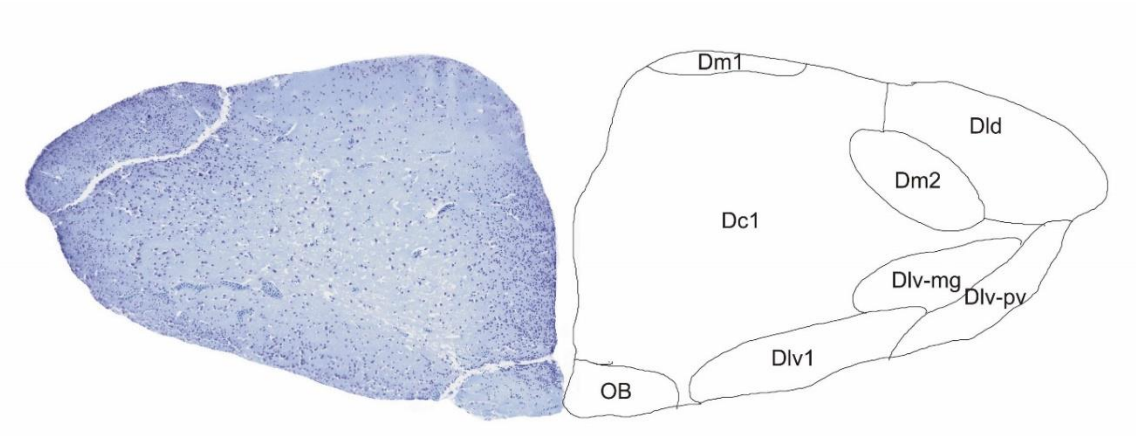

Fig. 1. Transverse section of *L.dimidiatus* telencephalon

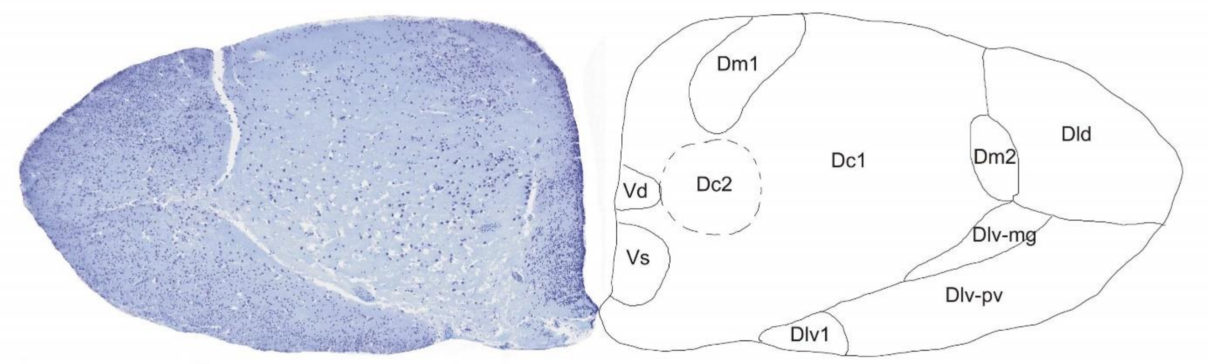

Fig. 2. Transverse section of *L.dimidiatus* telencephalon

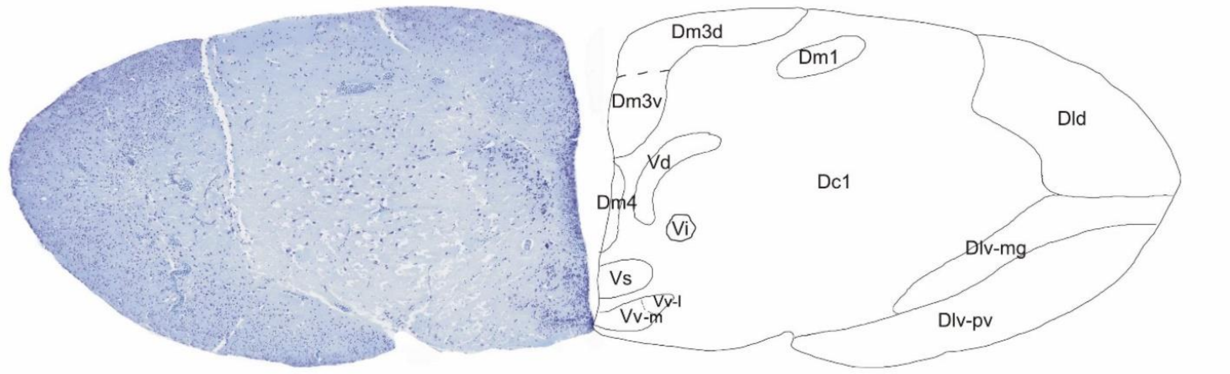

Fig. 3. Transverse section of *L.dimidiatus* telencephalon

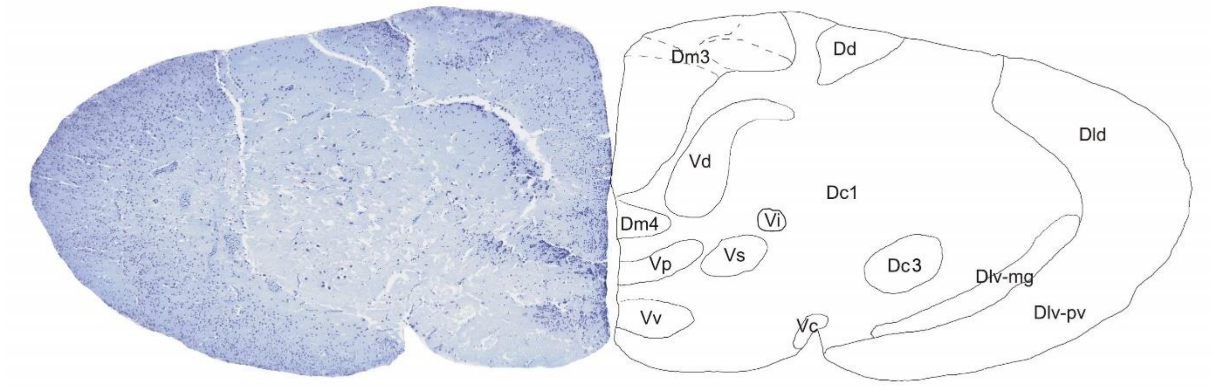

Fig. 4. Transverse section of *L.dimidiatus* telencephalon

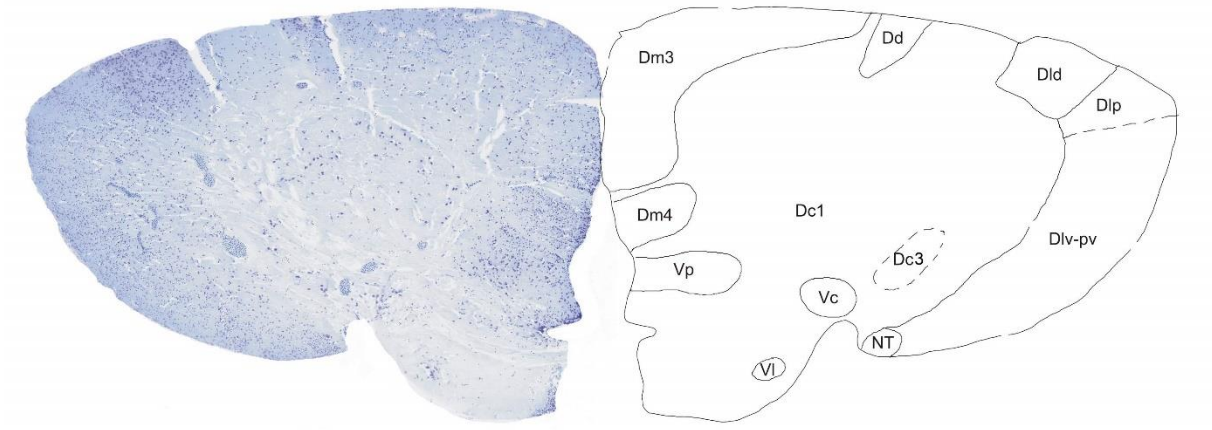

Fig. 5. Transverse section of *L.dimidiatus* telencephalon

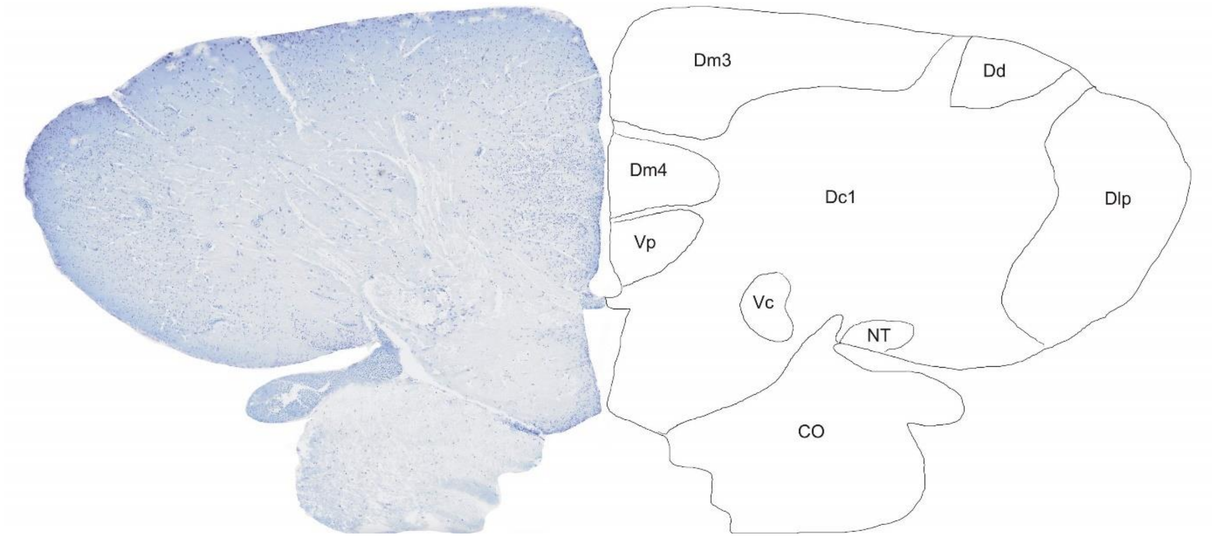

Fig. 6. Transverse section of *L.dimidiatus* telencephalon

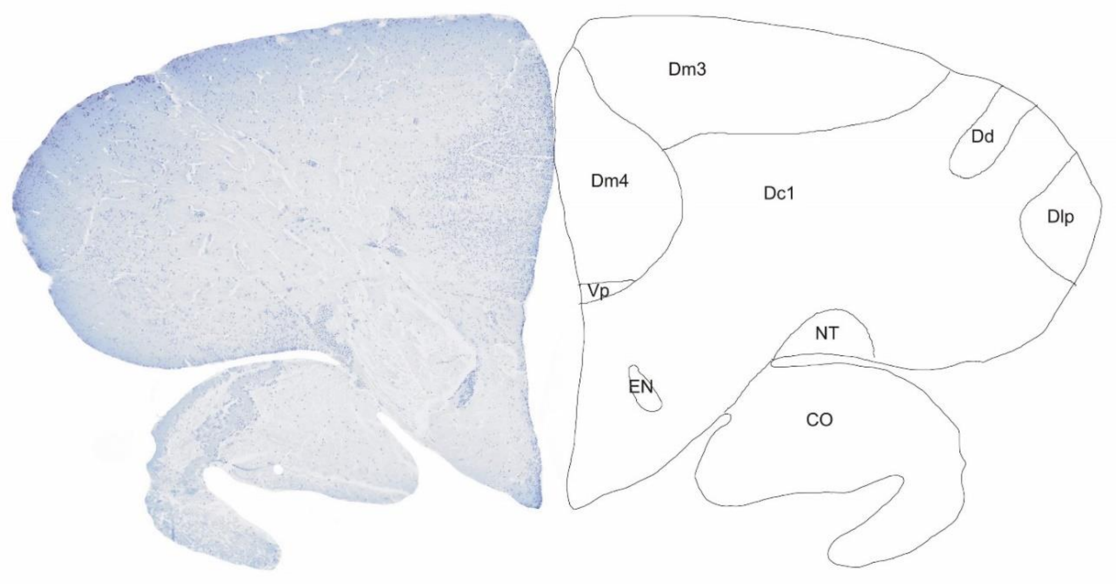

Fig. 7. Transverse section of *L.dimidiatus* telencephalon

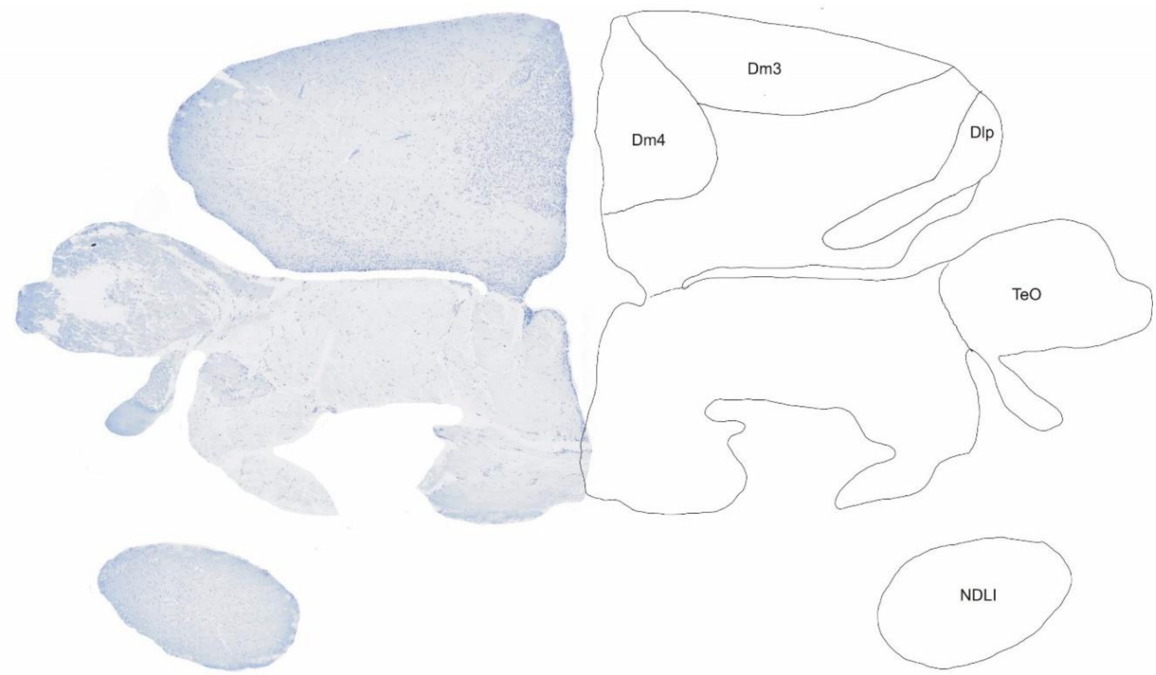

Fig. 8 Transverse section of *L.dimidiatus* telencephalon

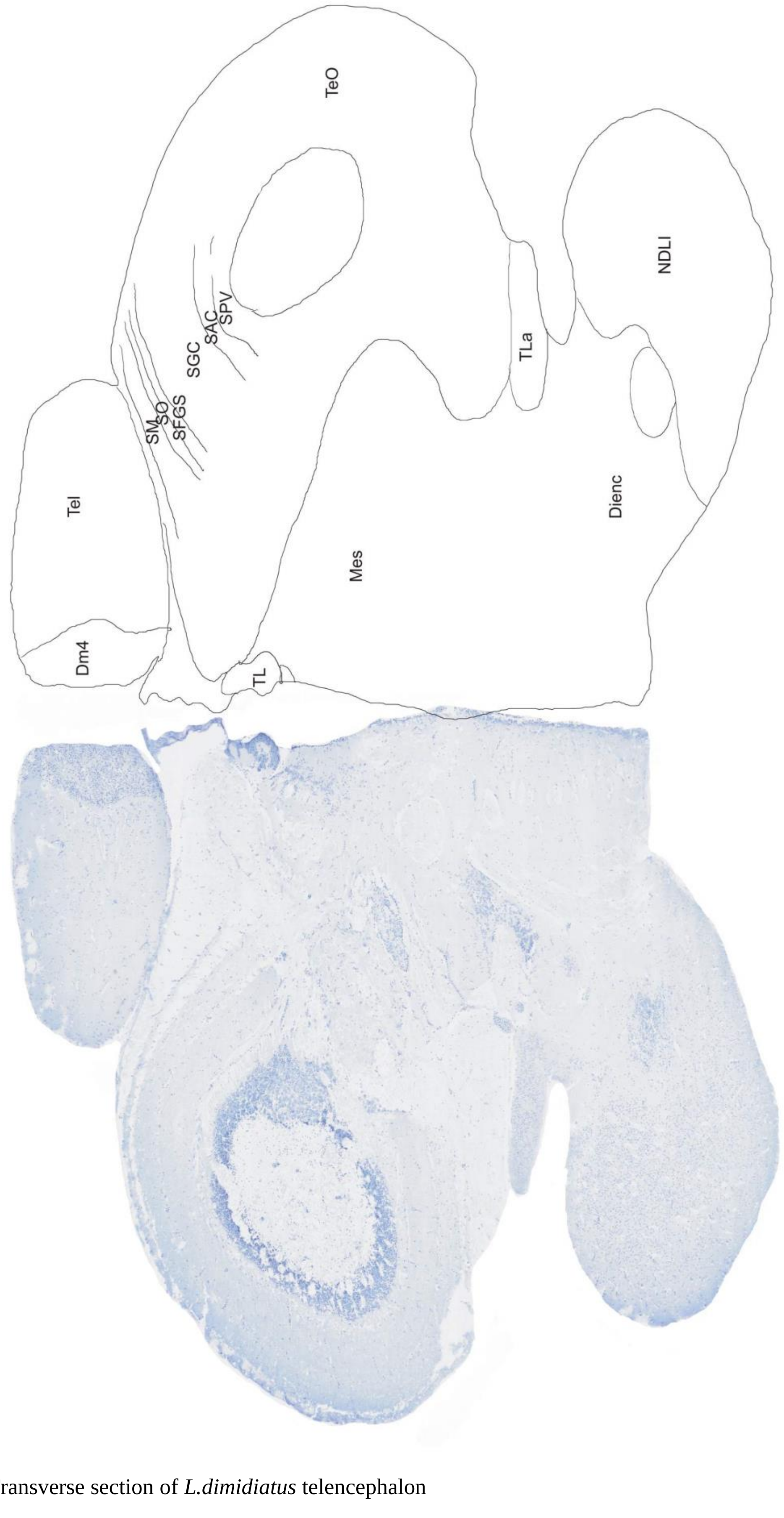

Fig. 9. Transverse section of *L.dimidiatus* telencephalon

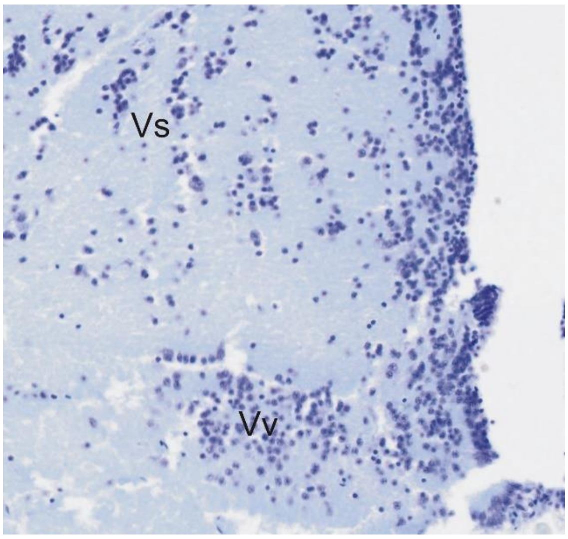

Fig. 10. Microphotography of transverse section of *L.dimidiatus* telencephalon showing nuclei Vs and Vv

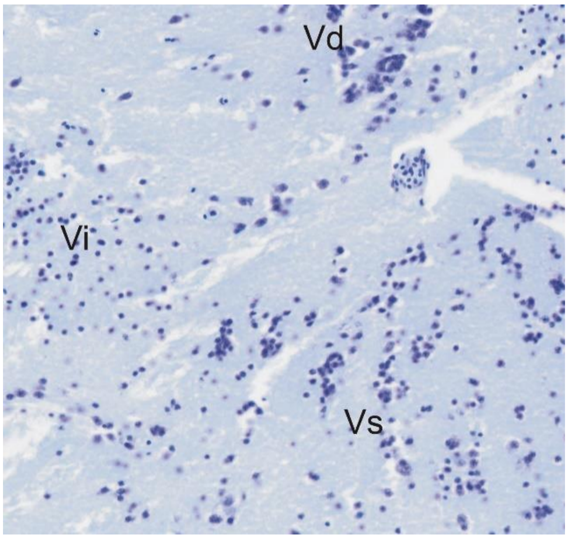

Fig. 11. Microphotography of transverse section of *L.dimidiatus* telencephalon showing nuclei Vd, Vs and Vi

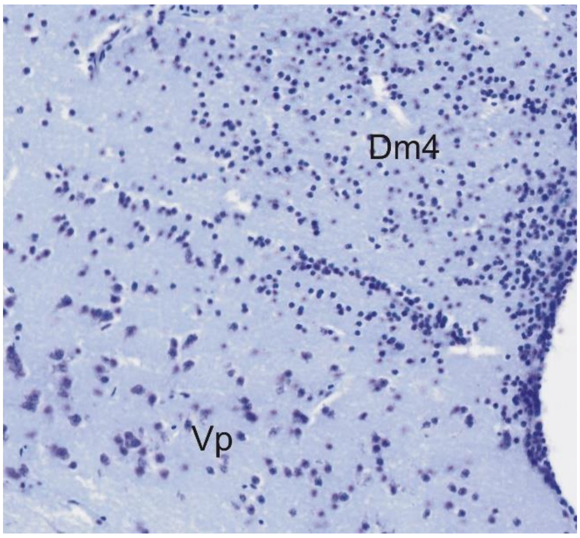

Fig. 12. Microphotography of transverse section of *L.dimidiatus* telencephalon showing nuclei Vp and region Dm4

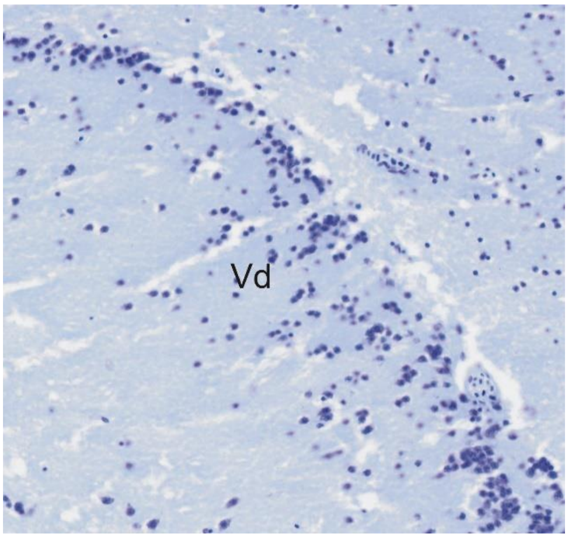

Fig. 13. Microphotography of transverse section of *L.dimidiatus* telencephalon showing nuclei Vd

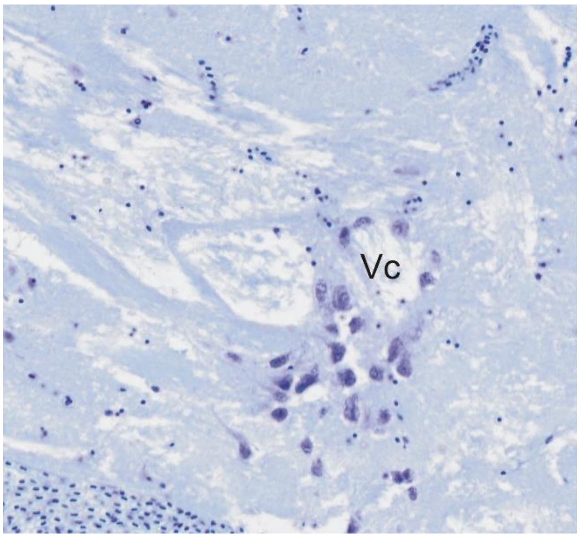

Fig. 14. Microphotography of transverse section of *L.dimidiatus* telencephalon showing nuclei Vc

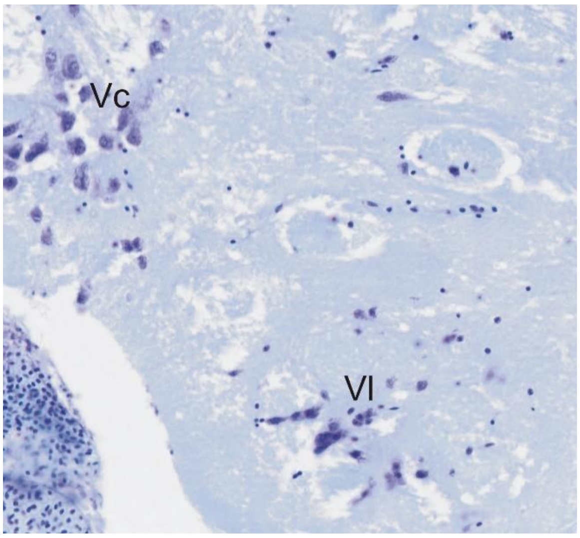

Fig. 15. Microphotography of transverse section of *L.dimidiatus* telencephalon showing nuclei Vc and Vl

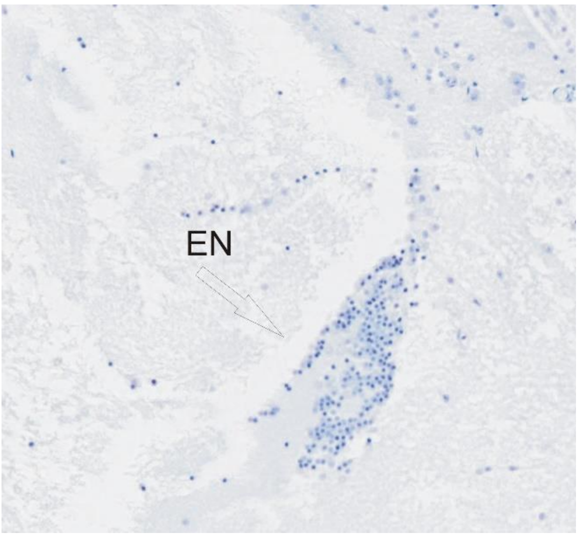

Fig. 16. Microphotography of transverse section of *L.dimidiatus* telencephalon showing nucleus entopeduncularis EN

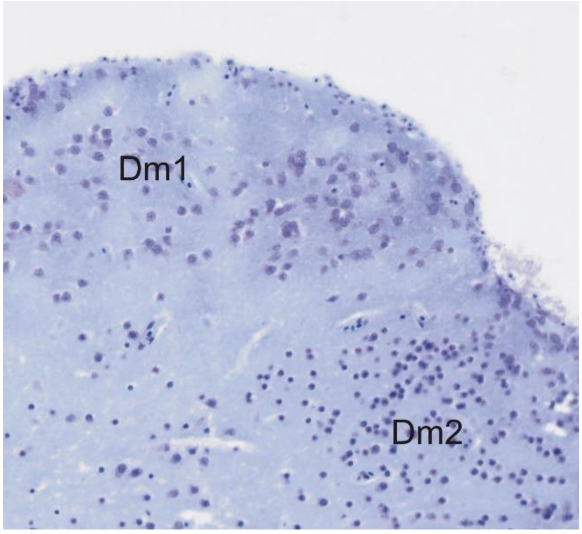

Fig. 17. Microphotography of transverse section of *L.dimidiatus* telencephalon showing regions Dm1 and Dm2

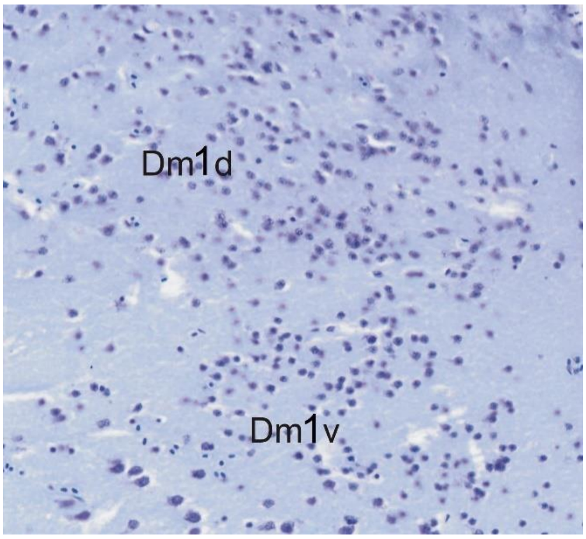

Fig. 18. Microphotography of transverse section of *L.dimidiatus* telencephalon showing subregions Dm1d and Dm1v

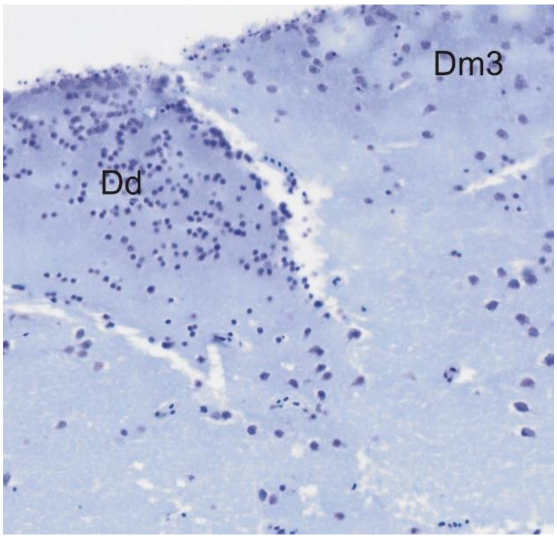

Fig. 19. Microphotography of transverse section of *L.dimidiatus* telencephalon showing region Dm3 and area Dd

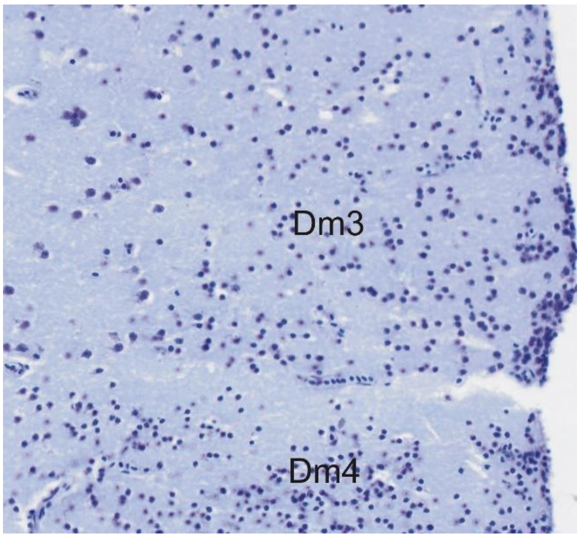

Fig. 20. Microphotography of transverse section of *L.dimidiatus* telencephalon showing regions Dm3 and Dm4

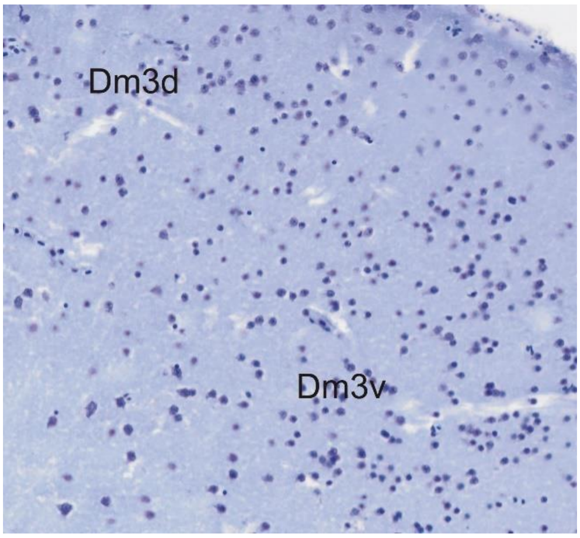

Fig. 21. Microphotography of transverse section of *L.dimidiatus* telencephalon showing subregions Dm3d and Dm3v

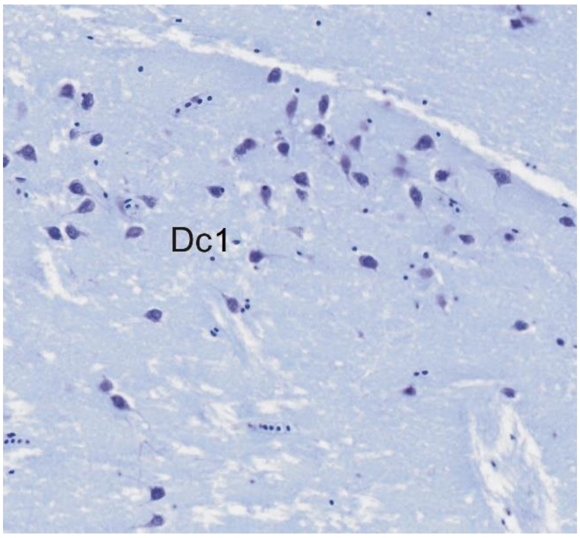

Fig. 22. Microphotography of transverse section of *L.dimidiatus* telencephalon showing region Dc1

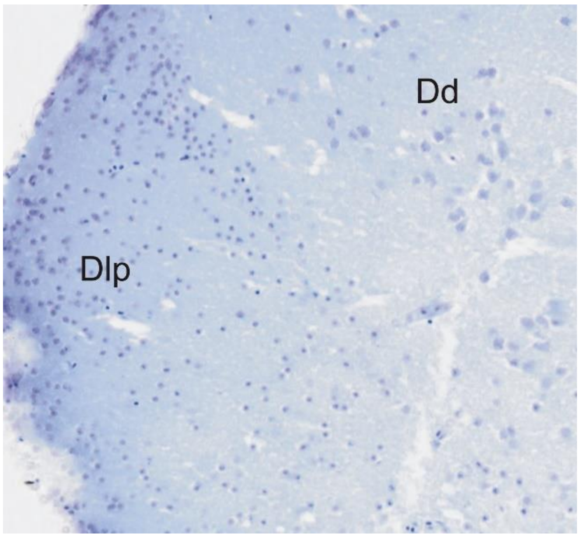

Fig. 23. Microphotography of transverse section of *L.dimidiatus* telencephalon showing area Dd and region Dlp

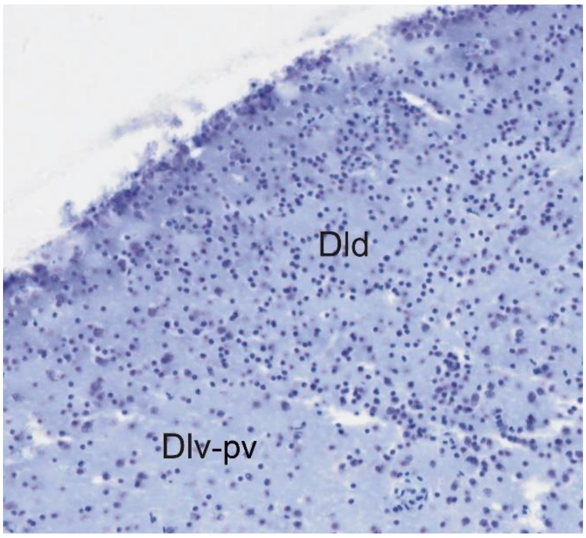

Fig. 24. Microphotography of transverse section of *L.dimidiatus* telencephalon showing region Dld and subregion Dlv-pv

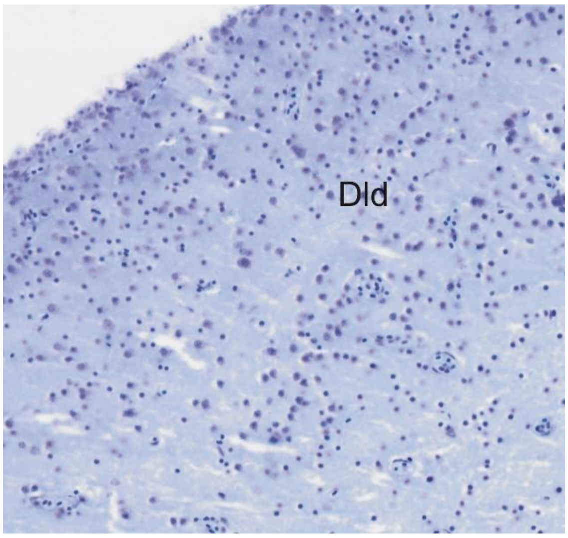

Fig. 25. Microphotography of transverse section of *L.dimidiatus* telencephalon showing region Dld

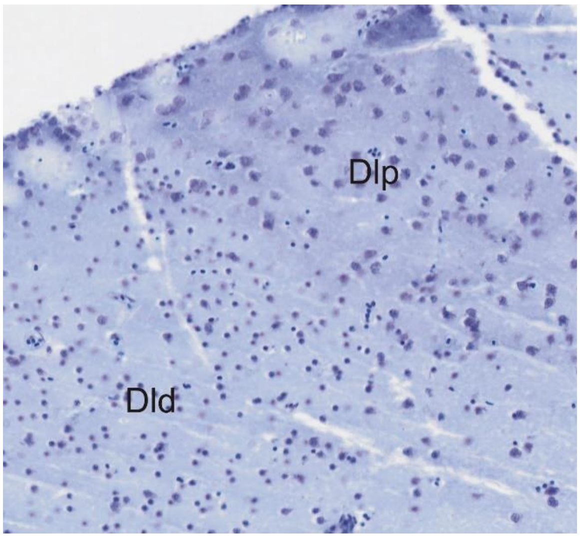

Fig. 26. Microphotography of transverse section of *L.dimidiatus* telencephalon showing region Dld and Dlp

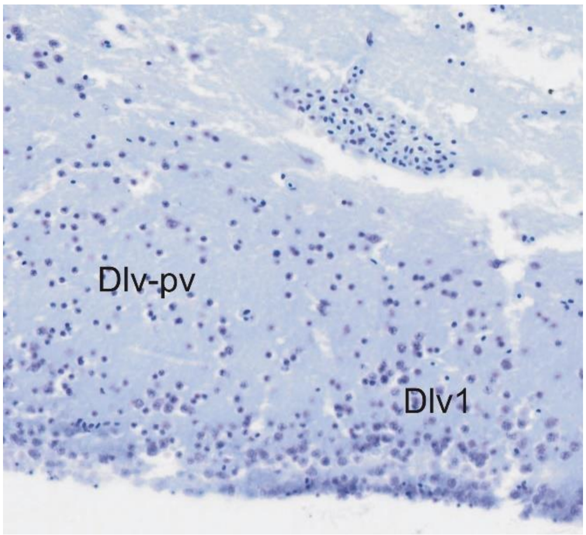

Fig. 27. Microphotography of transverse section of *L.dimidiatus* telencephalon showing subregions Dlv-pv and Dlv1

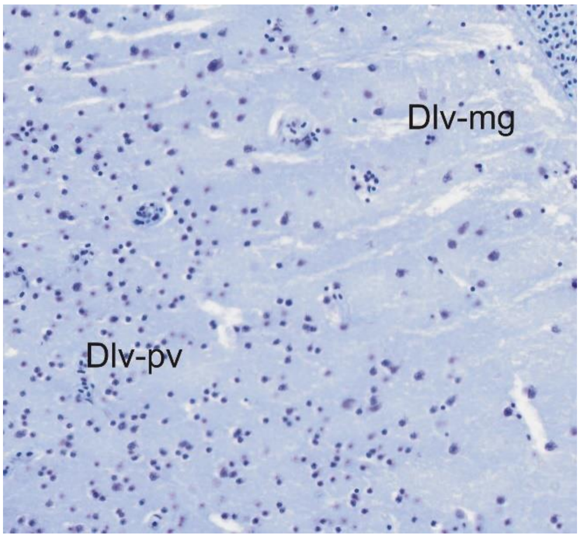

Fig. 28. Microphotography of transverse section of *L.dimidiatus* telencephalon showing subregions Dlv-pv and Dlv-mg

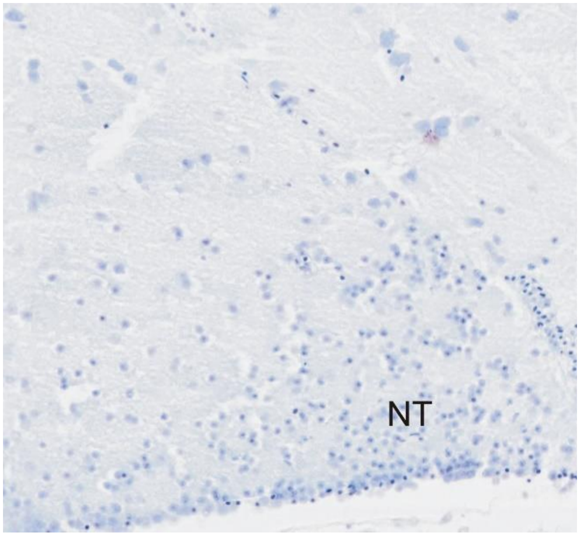

Fig. 29. Microphotography of transverse section of *L.dimidiatus* telencephalon showing nucleus taeniae NT

Tab 1. Nomenclature of *Labroides dimidiatus* nuclei and regions of the telencephalon.

D	dorsal part of the telencephalon
Dc	central area of dorsal telencephalon
Dd	dorsal area of dorsal telencephalon
Dl	lateral area of dorsal telencephalon
Dld	dorsal region of the lateral area of dorsal telencephalon
Dlp	posterior region of the lateral area of dorsal telencephalon
Dlv	ventral region of the lateral area of dorsal telencephalon
Dlv1	subregion 1 of the ventral region of the lateral area of dorsal telencephalon
Dlv-mg	subregion magnocellularis of the ventro-lateral area of dorsal telencephalon
Dlv-pv	subregion parvocellularis of the ventro-lateral area of dorsal telencephalon
Dm	medial area of dorsal telencephalon
Dm1	region 1 of the medial area of dorsal telencephalon
Dm1d	dorsal subregion of the region 1 of the medial area of dorsal telencephalon
Dm1v	ventral subregion of the region 1 of the medial area of dorsal telencephalon
Dm2	region 2 of the medial area of dorsal telencephalon
Dm2d	dorsal subregion of the region 2 of the medial area of dorsal telencephalon
Dm2v	dorsal subregion of the region 2 of the medial area of dorsal telencephalon
Dm3	region 3 of the medial area of dorsal telencephalon
Dm3d	dorsal subregion of the region 3 of the medial area of dorsal telencephalon
Dm3v	dorsal subregion of the region 3 of the medial area of dorsal telencephalon
Dm4	region 4 of the medial area of dorsal telencephalon
Dp	posterior area of dorsal telencephalon
EN	entopeduncular nucleus
GCL	granular cell layer of the olfactory bulb
GL	glomerular layer of the olfactory bulb
NT	nucleus taeniae
OB	olfactory bulb

Sy	sulcus ypsiloniformis
V	vental part of the telencephalon
Vc	nucleus commissuralis of the ventral part of the telencephalon
Vd	dorsal nucleus of the ventral part of the telencephalon
Vl	nucleus lateralis of the ventral part of the telencephalon
Vp	nucleus postcommissuralis of the ventral part of the telencephalon
Vs	nucleus supracommisuralis of ventral part of the telencephalon
Vv	ventral nucleus of the ventral part of the telencephalon
Vv-1	subnuncleus 1 of the ventral nucleus of the ventral part of the telencephalon
Vv-m	medial subnucleus of the ventral nucleus of the ventral part of the telencephalon

Tab. 2. List of species in which the analysis of telencephalon was conducted with the nuclei and regions recognized and nomenclature used.

	OB	Vd	Vs	Vv	Vp	Vi	Vl	Vn	Vc	EN	Dm	Dc	Dl	Dd	Dp	NT	LSO	
Polypterus senegalus	OB	Vd		Vv			Vl	Vn			DMPd DMPv DMPc		DLPm DLPl					
Polypterus palmas	ICL SOF ECL GL ON	Vd	Vs	Vv	Vp		Vl	Vn		Ed Ev Ec	DMPv (P1-v) DMPd (P1-d)		P3?	P2?				NOT
Lepisosteus osseus	ICL SOF ECL GL ON	Vd	Vs	Vv	Vp	Vi	Vl	Vn		Er Ec	Dm		Dl	Dd	Dp	NT		
Anguilla japonica	ICL ECL GL	Vd	Vs	Vv	Vp		Vl				Dm	Dc	Dl Dld Dlv	Dd				
Barbus meridionalis		Vd	Vs	Vv	Vp	Vi				NE	Dma Dmp Dmpd Dmpv	Dcm Dcd Dcl	Dl Dld Dlv Dlp	Dd		NT		
Carassius auratus		Vd	Vs	Vv	Vp		Vl			NE	Dm	Dc	Dl Dlv Dld	Dd		NT		
Tinca tinca		Vd	Vs	Vv		Vi	Vl			NE	Dm	Dc	Dl	Dd				
Danio rerio	POF GL ECL ICL	Vd		Vv	Vp		Vl1 Vl2		Vc	ENv ENd	Dm	Dc	Dl	Dd	Dp	NT		
Gymnotus carapo	ICL	Vd	Vs	Vv	VP		Vl		Vc	Er	DM1 DM2v DM2c	DC	DLv DLd DLp	DD DDmg	DP	nT		
Apteronotus leptorhynchus	ICL	Vd	Vs	Vv	Vp	VI VId VIr	Vl	Vn	Vc	Er Ec	DM1 DM2r DM2v DM2c Dm2d	DC	DLd DLv Dlp	DD DDs DDi DDmg	DP DPl DPm	nT		
Ictalurus punctatus	ICL SOF MCL GL ON	Vd Vd-d Vd-v	Vs	Vv Vv-v Vv-d	Vp	Vi	Vl	Vn	Vc	Ed Ev	DM	DC-1 DC-2 DC-3	DLd DLv Dlp	Dd	DP DPr DPc	NT		
Salmo gairdneri	ICL SOF ECL GL	Vd	Vs	Vv	Vp		Vl		Vc	E	Dm Dm-1 Dm-2 Dm-3 Dm-4	Dc	Dl-d Dl-v Dl-p	Dd (Dd + Dl-d)	Dp	NT		
Oncorhynchus keta		Vd		Vv		Vir	St?				Dm2d Dm2v	Dc	Dl	Dd		nT		

Oryzias latipes		Vd	Vs	Vv	Vp	Vi	Vl			NE	Dm vDm dDm	Dc	Dl dDl vDl		Dp			
Fundulus heteroclitus	TN GL ON	Vd	Vs	Vv	Vp		Vl			NE	Dm	Dc Dcd	Dl Dll Dlv Dld	Dd		NT		
Xiphophorus helleri		Vd	Vs	Vv	Vp	Vi	Vl		Vc	E	Dm1 Dm2 Dm3 Dm4	Dc Dc1 Dc2 Dc3 Dc4	Dlv Dld Dll Dlp	Dd	Dp	NT	ON?	
Nothobranchius furzeri	ECL ICL GL	Vd	Vs	Vv	Vp		Vl		Vc	Ed Ev	Dm1 Dm2 Dm3 Dm4	Dc1 Dc2 Dc3 Dc4	Dld Dlv Dll	Dd		NT		
Sebasticus marmoratus		Vd	Vs		Vp	Vi	Vl				dDm vDm	Dc	dDl vDl	Dd	Dp			
Paraliparis devriesi	ICL ECL SOF Gl	Vd		Vv			Vl		Vc	E	Dm	Dc	Dl	Dd	Dp			
Toxotes chatareus	GL ICL pof	Vd	Vs	Vv	Vp		Vl		Vc	EN	Dmd Dmv	Dc	Dld Dlv Dlp	Dd	Dp		LSO	
Dolloidraco longedorsalis		Vd	Vs	Vm?			Vl				Dm	Dc	Dl	Dd	Dp	NT		

Rhyacichthys aspro		v.d.		v.v.			v.l.			N.e.	d.m.	d.c.	d.l.	d.d.	d.p.			N.i.
Betta splendens	Icl	Vd	Vs	Vv	Vp	Vi	Vl		Vc	NE	Dmd Dmv	Dc1 Dc2 Dc3 Dc4	Dlv Dld Dlp	Dd	Dp	NT		
Channa gachua	GCL MCL GL ONL	Vd	Vs	Vv	Vp	Vi	Vl		Vc	NE	Dm1 Dm2 Dm3 Dm4	Dc1 Dc2	Dld Dlv1 Dlv2 Dld Dlp	Dd	Dp	NT	LSO	
Oreochromis mosambicus	BOgl BOgra	Vd	Vs	VVm							DMa DMdd DMdv DMvd DMvv		DLs DLv DLd DLp	DD	Dp			DA
Oreochromis niloticus					Vp	Vi				E	dDm vDm		Dl		Dp			
Astatotilapia (Haplochromis) burtoni		Vd	Vs-lVs-m	Vv	Vp	Vi	Vl		Vc		Dm-1 Dm-2r Dm-2c Dm3	Dc-1 Dc-2 Dc-3 Dc-4 Dc-5	Dl-d Dl-v1 Dl-v2 Dl-g	Dd-d Dd-v	Dp	NT		Dx
Labroides dimidiatus	GCL GL	Vd	Vs	Vv Vv-m Vv1	Vp	Vi	Vl		Vc	EN	Dm1 Dm1d Dm1v Dm2 Dm3 Dm3d Dm3v Dm4	Dc1 Dc2 Dc3	Dlv1 Dlv-pv Dlv-mg Dld Dlp	Dd	NT			

Lepomis cyanellus	ICL SOF ECL GL ON TN	Vd	Vs	Vv	Vp	Vi	Vl		Vc	NE (E)	Dmd Dmv (Dm-1 Dm-2 Dm-3 Dm-4)*	(Dc-1 Dc-2 Dc-3 Dc-4)	Dld Dlv Dlp (Dl-d Dl-v Dl-p)*	Dd	Dp	NT		
Dicentrarchus labrax	OLN GL ECL SOF ICL	Vd	Vs	Vv	Vp	Vi	Vl		Vc	E		Dc1 Dc2	Dlv1 Dlv2 Dld Dlp	Dd	Dp	NT	LSO	
Chaetodon multicinctus	ONF GL ECL SOF ICL	Vd	Vs	Vv	Vp	Vi	Vl		Vc	E	Dm1 Dm2 Dm3 Dm4	Dc1 Dc2	Dld Dlv1 Dlv2 Dlv3 Dlp Dx	Dd	Dp	NT		Vu
Sparus aurata	ICL SOF ECL OIN TNgc	Vd	Vs	Vv	Vp	Vi	Vl		Vc	NE	Dm1 Dm2 Dm3 (hypertrophy) Dm4	Dc1 Dc2	Dlv1 Dlv2 Dlv3 Dld Dlp	Dd	Dp	NT	LSO	
Protopterus annectens	ON G M P IG MZ		Sm			Si	Sl		Sc		Py pi pd			pp				

OB – olfactory bulb

- ECL – external cellular layer of olfactory bulb
- GL, Gl, BOgl, G, GCL – glomerular layer of the olfactory bulb
- ICL, Icl – internal cellular layer of olfactory bulb
- IG, BOgra – granular layer of the olfactory bulb
- M, MI - Mitral cell layer of the olfactory bulb
- MCL, OIN, TNgc, OLN, ONL – additional divisions of the OB
- MZ – marginal zone of the olfactory bulb
- ON – olfactory nerve layer of the olfactory bulb olfactory nerve fibers
- P - internal plexiform layer of the olfactory bulb
- POF, pof – primary olfactory fiber layer
- SOF – secondary olfactory fiber layer of the olfactory bulb

Vd, v.d. – dorsal nucleus of the ventral telencephalon (subnuclei Vd-v, Vd-d)

Vs, lVs-m, Sm, – supracommissural nucleus of the ventral telencephalon (subnuclei Vs-l, Vs-m)

Vv, v.v., VVm, Vm –ventral nucleus of the ventral telencephalon (subnuclei Vv-d, Vv-v)

Vp, VP, - postcommissural nucleus of the ventral telencephalon

Vi, Vir, Si, VI, N.i.– nucleus intermedius of the ventral telencephalon (subnuclei VId Vir)

Vl, v.l., Sl, L. - lateral nucleus of the ventral telencephalon

Vn - ‘nother nucleus of ventral telencephalon

Vc, Sc –commissural nucleus of the ventral telencephalon

EN, N.e., n.e., NE, E – Entopeduncular nucleus (subnuclei Ed, Ev, Er, Ec)

Dm, Dm (1, 2, 3, 4) D.m. d.m. DM1 Dm-1 – medial area of the dorsal telencephalon (subdivisions Dma, Dmd, dDm, Dmv, vDm, DMdd, DMdv, DMvd, DMvv, Dmp, Dmpd, Dmpv, Dm-2r, Dm-2c, DM2c, Dm2d, DM2r, Dm2v, DM2v)

Dc, d.c. – central area of the dorsal telencephalon (subdivisions Dc1, Dc2, Dc3, Dc, Dcd, Dcl, Dcm)

Dl, d.l. – lateral area of the dorsal telencephalon (subdivisions Dld, Dl-d, d-Dl, DLd, Dlv, Dlv1, Dlv2, Dlv3, Dl-v, vDl, Dl-v1, Dl-v2 ,Dlp, Dl-p, DLp, DLPm, DLPl, Dll, Dl-g, DLs, DLa)

Dd, DD, D-d, d.d., pp. – dorsal area of the dorsal telencephalon (subdivisions DDmg, DDs, DDi, Dd-d Dd-v)

Dp, D.p. d.p. – posterior area of the dorsal telencephalon

NT, nT, TN– nucleus taeniae

LSO – lateral septal organ

P2 – second pallial zone

P3 – third pallial zone

pd - Pars dorsalis of the medial pallium

pi - Pars intermedius of the medial pallium

pp - pars profundus of the rostral dorsal pallium

ps - pars superficialis of the rostral dorsal pallium

pv - Pars ventralis of the medial pallium

Sc - central subpallium

Si - superficial isthmic nucleus

Sl - lateral subpallium

Sm - medial subpallium

DA – anterior part of the dorsal telencephalon

Dx – large-cell division of the lateral zone of the dorsal telencephalon

LP - lateral pallium

MP - medial pallium

NOT – nucleus of the olfactory tract

Tab. 3. List of species organized according to phylogenetic relationships in which the analysis of the telencephalon was conducted.

- Actinopterygii
  - Cladistia
    - Polypteriformes
      - Polypteridae *Polypterus senegalus* (Reiner and Northcutt, 1992)
        - *Polypterus palmas* (Reiner and Northcutt, 1992)
  - Neopterygii
    - Lepisosteiformes
      - Lepisosteidae *Lepisosteus osseus* (Northcutt and Braford, 1980)
    - Teleostei
      - Anguiliformes
        - Anguilidae *Anguilla japonica* (Makuda and Ando, 2003)
      - Cypriniformes
        - Cyprinidae *Barbus meridionalis* (Diez et al., 1987)
          - *Carassius auratus* (Peter and Gill, 1975)
          - *Tinca tinca* (Arevalo et al., 1992)
          - *Danio rerio* (Wullimann, 1996)
      - Gymnotiformes
        - Gymnotidae *Gymnotus carapo* (Corrêa et al., 1998)
        - Apteronotidae *Apteronotus leptorhynchus* (Maler et al., 1991)
      - Siluriformes

Ariidae *Ictalurus punctatus* (Bass, 1981)
Salmoniformes
Salmonidae *Salmo gairdneri* (Northcutt and Braford, 1980)
Oncorhynchus keta (Pushina et al., 2003)
Beloniformes
Adrianichthyidae *Oryzias latipes* (Ishikawa et al. 1999)
Cyprinodontiformes
Fundulidae *Fundulus heteroclitus* (Peter et al., 1975)
Poeciliidae *Xiphophorus helleri* (Anken and Rahmann, 1994)
Aplocheilidae *Nothobranchius furzeri* (D'Angelo 2013)
Scorpaeniformes
Scorpaenidae *Sebasticus marmoratus* (Murakami et al., 2005)
Liparidae *Paraliparis devriesi* (Eastman and Lanoo, 1998)
Perciformes
Toxotidae *Toxotes chatareus* (Karoubi et al 2016)
Artedidraconidae *Dolloidraco longedorsalis* (Eastman and Lanoo, 2003)
Rhyacichthyidae *Rhyacichthys aspro* (Bauchot et al., 1989)
Osphronemidae *Betta splendens* (Marino-Neto and Sabbatini, 1988)
Channidae *Channa gachua* (Baile and Patle 2011)
Cichlidae *Oreochromis mosambicus* (Simoes et al. 2012)
Oreochromis niloticus (Yoshimoto et al 1998)
Astatotilapia (Haplochromis) burtoni (Burmeister et all 2009)
Labridae *Labroides dimidiatus*
Centrarchiformes
Centrarchidae *Lepomis cyanellus* (Northcutt and Braford, 1980)
Moroniformes
Moronidae *Dicentrarchus labrax* (Cerdá-Reverter et al., 2001)
Chaetodontiformes
Chaetodontidae *Chaetodon multicinctus* (Dewan and Tricas 2013)
Spariformes
Sparidae *Sparus aurata* (Munoz-Cueto et al., 2001)

Sarcopterygii
Ceratodontiformes
Protopteridae: *Protopterus annectens* (Reiner and Northcutt, 1987)

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