Gross brain morphology of
Rhamdia quelen (Quoy & Gaimard 1824)
(Ostariophysi: Siluriformes: Heptapteridae)

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Abstract. The brain gross morphology of *Rhamdia quelen* is described and compared with seven species of six genera of Heptapteridae. Interspecific variation in shape, size, and position of brain subdivisions was observed in all examined species. The posterior position of the *hypophysis* on the *hypothalamus* and presence of a lateral subdivision on the *lobus facialis* are shared by all examined heptapterids. *Rhamdia quelen* and *Pimelodella gracilis,* currently considered closely related within the family Heptapteridae, exhibit the anterior and posterior area of the *telencephalon* with equivalent widths, and the lateral line lobe reaching the anterior area of the *lobus vagi*. Members of the so called *Nemuroglanis* sub-clade (*Cetopsorhamdia iheringi, Heptapterus mustelinus, Imparfinis mirini,* and *Phenacorhamdia tenebrosa*) share the *lobus vagi* proportional smaller than the *lobus facialis;* the lateral line lobe reaching the half length of the *lobus facialis;* the *tectum mesencephali* in contact with the *telencephalon,* and thinner anterior area of the *telencephalon*. The results reveal several features that are phylogenetically informative among the heptapterids examined, and corroborate previous hypotheses based on other non-neural anatomical characters.

Key-Words. Central nervous system; Anatomy; Catfish; Neotropical region.

INTRODUCTION

Siluriformes is a diverse order of the Otophysi, widely distributed across the globe, mainly throughout the tropical regions. It presents a high morphological diversity, especially when compared to its close relatives, the Characiformes and Cypriniformes (Rosen & Greenwood, 1970; Fink & Fink, 1981; Howes, 1983; Ferraris Jr., 2007). However, despite this wide morphological disparity, studies on the brains of Neotropical catfishes have been largely neglected; as opposed to what happens with the North American ictalurids where its neuroanatomy is relatively better understood (Herrick & Herrick, 1891; Atema, 1971; Lundberg, 1982; Tong & Finger, 1983; Meek & Nieuwenhuys, 1998). To date, there are few studies published on gross brain morphology of neotropical catfishes (*e.g.,* Rosa *et al.,* 2014 on *Otothyris;* Abrahão & Shibatta, 2015 on *Pseudopimelodus bufonius;* Angulo & Langeani, 2017 on *Rineloricaria heteroptera;* and Abrahão *et al.,* 2018 on Pseudopimelodidae).

Among Siluriformes, Heptapteridae currently includes 218 valid species of small to medium-sized catfishes distributed in 24 genera (Eschmeyer & Fong, 2018). They live among rocks and logs on river bottoms, associated to marginal vegetation or buried in sand (Bockmann & Guazelli, 2003). The family was first proposed a monophyletic group within the Pimelodidae by Lundberg & McDade (1986), and later corroborated by Ferraris Jr. (1988) and Lundberg *et al.* (1991), in which members of the Heptapteridae were included in the subfamily Rhamdiinae. Recent studies regarding the phylogenetic relationships on catfishes, based on molecular analysis, have proposed that the Heptapteridae is more related to a clade composed by the Pimelodidae, Pseudopimelodidae and *Conorhynchos* (Hardman, 2005; Sullivan *et al.,* 2006; Sullivan *et al.,* 2013). Bockmann (1998), on the other hand, was the first to propose a more encompassing phylogenetic relationship of the Heptapteridae, recognizing some synapomorphies, based on the external morphology and osteology, for several species groups.

In the Heptapteridae, the genus *Rhamdia* Bleeker 1858 can be diagnosed by a unique combination of nine characters (Silfvergrip, 1996), and nowadays includes 27 species (Eschmeyer

Table 1. Morphometric data of major subdivisions of the brain of members of the Heptapteridae. Total length of brain (BL) in millimeters, other characters in proportions of BL. SD = Standard deviation; n = number of specimens.

Measurements	G. eques (n = 2)	G. eques Mean ± SD	C. iheringi (n = 1)	H. mustelinus (n = 3)	H. mustelinus Mean ± SD	I. mirini (n = 3)	I. mirini Mean ± SD	P. tenebrosa (n = 1)	P. gradilis (n = 4)	P. gradilis Mean ± SD	R. quelen (n = 6)	R. quelen Mean ± SD
Total Length (mm)	7.4-7.9		6.8	5.3-6.3		6.6-8.3		5.8	9-10.8		14.6-15.8	
Medulla oblongata	7.3-7.8	7.5 ±0.3	7.2	6.1-6.8	6.4 ±0.3	7.7-8.2	7.9 ±0.2	7.5	8.6-10	9.4 ±0.6	7.5-8.4	7.9 ±0.4
Lobus vagi	15.7-18	16.8 ±1.5	13.2	12.6-12.8	12.7 ±0.2	13.9-15.9	14.9 ±0.2	12.3	16-17.3	16.8 ±0.6	15.8-16.3	16.1 ±1.4
Lobus facialis	13.2-15.5	14.4 ±1.7	19.5	19.9-19.6	19.8 ±0.3	16.2-16.6	16.4 ±0.2	17.5	10.3-13.2	11.6 ±1.2	14.5-14.9	14.6 ±0.2
Lobus lineae lateralis	13.3-14.9	14.1 ±1.1	11	10.2-10.6	10.4 ±0.2	9.9-10.9	10.4 ±0.6	12	14.5-16.4	15.4 ±0.8	13.1-13.2	13.2 ±0.05
Corpus cerebelli	39.2-40.6	39.9 ±1	55.7	59.4-58.6	59.1 ±0.4	37.2-42.7	39.9 ±0.4	49.7	47.3-52.8	50.1 ±2.4	45.1-48.6	47.4 ±1.9
Tectum mesencephali	28.7-30.6	29.6 ±1.3	26.8	28.1-28.6	28.3 ±0.2	23.9-26.8	25.3 ±0.7	23.9	27.9-32.3	30.1 ±2	24.8-26.4	25.5 ±0.8
Hypothalamus	30.5-32.5	31.4 ±1.1	34.8	37.1-37.8	37.5 ±0.3	31.2-33.8	32.5 ±1.8	34.7	32.9-35.2	34 ±1.2	29.1-30.3	29.9 ±0.6
Telencephalon	31.9-32.4	32.2 ±0.3	31.2	30.8-31.8	31.2 ±0.5	29.3-30.2	29.7 ±1	32.5	31.4-35.6	33.1 ±1.9	30.6-31.4	31.1 ±0.4

& Fong, 2018). *Rhamdia quelen* (Quoy & Gaimard, 1824) is widely distributed from northern Mexico to southern South America, in both cis- and trans-Andean watersheds, and is one of the most interesting taxa in the genus due to sympatric and even syntopic occurrence with other congeners. Although the ubiquitous distribution throughout the neotropical region, the complicated taxonomic history and the vast list of synonymies, the species can be distinguished by a set of 12 character states (Silfvergrip, 1996). However, there is disagreement as to the validity of these characters that can embrace several different morphotypes under a single name (Angrizani & Malabarba, 2018).

The fish brains exhibit a great plasticity that can also be found within specialized organs that are strongly correlated to environmental changes and behavioral adaptations in niches (Kleerekoper, 1969; Ito *et al.*, 2007), demonstrating that similar environments often lead to similar solutions (Kotrschal *et al.*, 1998). This results in some divergent morphological patterns found among phylogenetic distant taxa (Kotrschal & Palzenberger, 1992; Eastman & Lannoo, 1995; van Staaden *et al.*, 1995; Ito *et al.*, 2007). However, some recent works on neotropical fish brains in a systematic framework show evidences that several sub-units have their shape due to shared evolutionary history rather than ecology (Gonzalez-Voyer & Kolm, 2010; Pupo, 2011; Abrahão, 2013; Pereira, 2014; Pupo, 2015; Abrahão *et al.*, 2018).

Few studies on morphological diversity within the Heptapteridae have been published to date (*e.g.*, Lundberg & McDade, 1986; Silfvergrip, 1996; Bockmann & Miquelarena, 2008; Slobodian & Bockmann, 2013), and the literature is even scarce when concerning the brain gross morphology of this group. Herein, the brain gross morphology and major cranial nerves of the *R. quelen* are described. Anatomical including seven other representatives of the family Heptapteridae are also made. Finally, intrafamiliar characters evolution is discussed.

MATERIAL AND METHODS

Brain gross morphology was obtained from six dissected specimens of *R. quelen* (187.4-222.3 mm SL) and compared to seven other species of the Heptapteridae. Dissections were performed following Abrahão & Pupo (2014) and Abrahão & Shibatta (2015). A digital camera attached to a stereoscopic microscope was used to capture images of the brain topography. Measurements of the major brain topographic units were taken on digital images, using the software Axio Vision Rel v.4.8 (Carl Zeiss Axio Vision Product Suite), and are expressed and presented as proportions of the total brain length (BL), see Table 1. Total brain length was measured from the rostral portion of the *telencephalon* to the most caudal portion of the *lobus vagi* (modified from Lannoo & Eastman, 2000). Only the *lobus inferior hypothalami* was measured in the *diencephalon,* because this region has visible topography and with well-defined boundaries. Neuroanatomy nomenclature follows Meek & Nieuwenhuys (1998) and

Butler & Hodos (2005). Osteological nomenclature follows Silfvergrip (1996), Bockmann (1998), and Arratia *et al.* (2003). Brains were kept in 4% formalin buffered with CaCO₃, after removal from the neurocranium. All specimens were preserved in 70% ethanol after fixation in 4% formalin. The software R (R Core Team, 2017) was used to perform the statistical analysis.

Material examined

All specimens are deposited at the Museu de Zoologia da Universidade Estadual de Londrina (MZUEL) and the Museu de Zoologia da Universidade de São Paulo (MZUSP). Specimens are designated as ALC (alcohol), SK (dry skeleton), or C&S [cleared and double stained according to Dingerkus & Uhler (1977)]. *Cetopsorhamdia iheringi* Schubart & Gomes, 1959. MZUEL 2260 (2 ALC: 50.8-51.9 mm SL). *Goeldiella eques* (Müller & Troschel, 1849). MZUEL 7417 (2 ALC: 57.1-64.9 mm SL). *Heptapterus mustelinus* (Valenciennes, 1835). MZUEL 5074 (3 ALC: 66.1-63.4 mm SL). *Imparfinis mirini* Haseman, 1911. MZUEL 5765 (1 ALC: 83.2 mm SL). MZUEL 4028 (2 ALC: 50.6-51.6 mm SL). *Phenacorhamdia tenebrosa* (Schubart, 1964). MZUEL 2706 (2 ALC: 65.1-66.1 mm SL). *Pimelodella gracilis* (Valenciennes, 1835). MZUEL 1574 (4 ALC: 117.6-132.2 mm SL). *Rhamdia quelen*. MZUEL 6036 (6 ALC: 187.4-222.3 mm SL); MZUEL 7418 (1 C&S: 61 mm SL); MZUEL 7455 (1 SK: 163.27 mm SL).

Comparative material: *Batrochoglanis raninus* (Valenciennes 1840). MZUEL 6035 (1 ALC: 76.7 mm SL). MZUSP 23407 (2 ALC: 51.4-76.6 mm SL). *Cephalosilurus fowleri* Haseman 1911. MZUEL 6040 (1 ALC: 275 mm SL). *Conorhynchos conirostris* (Valenciennes 1840). MZUEL 6673 (1 ALC: 390.0 mm SL). *Diplomystes mesembrinus* (Ringuelet 1982). MZUSP 62595 (1 ALC: 79.0 mm SL). *Ictalurus punctatus* (Rafinesque 1818). MZUEL 6671 (3 ALC: 78.87-82.34 mm SL). *Lophiosilurus alexandri* Steindachner 1876. MZUEL 5377 (1 ALC: 53.7 mm SL). MZUSP 96276 (1 ALC: 73.1 mm SL). *Microglanis cottoides* (Boulenger 1891). MZUEL 6033 (3 ALC: 40.1-48.8 mm SL). *Phreatobius sanguijuela* Fernández, Saucedo, Carvajal-Vallejos & Schaefer 2007. MZUEL 6486 (1 ALC: 39.0 mm SL). *Pimelodus maculatus* Lacepède 1803. MZUEL 1343 (3 ALC: 181.7-243.2 mm SL). *Pseudopimelodus mangurus* (Valenciennes 1835). MZUEL 2795 (2 ALC: 138.9-175.4 mm SL). *Steindachneridion parahybae* (Steindachner 1877). MZUEL 5231 (1 ALC: 262.4 mm SL). *Zungaro zungaro* (Humboldt 1821). MZUEL 6044 (1 ALC: 158.8 mm SL). MZUEL 6049 (1 ALC: 181.4 mm SL).

RESULTS

Measurements of the major brain subdivisions of the species examined are presented in Table 1. The brain is completely located beneath the supraoccipital and frontal bones, and above the parasphenoid and prootic in species of Heptapteridae, with exception of the *bulbus olfactorius* and part of the anterior portion of the *telencephalon* (Fig. 1).

Rhombencephalon

In all species examined the *medulla oblongata* is located posterior to the efferent projections of the *nervus vagus* to the *medulla spinalis* and is positioned dorsal to the *truncus cerebri*. The anterior portion lies posterolateral to the *lobus vagi,* and is positioned above the parasphenoid-basioccipital suture, beneath the supraoccipital process (Fig. 1). The *medulla oblongata* is topographically composed of two ovoid-shaped structures contacting the *medulla spinalis*. The posterior portion of the *medulla oblongata* is slightly thinner than their counterparts (Fig. 2). In *Rhamdia quelen* (Fig. 2), *Imparfinis mirini,* and *Phenacorhamdia tenebrosa* (Fig. 3), the *medulla oblongata* does not possess a conspicuous bulge posterolateral to the *lobus vagi*. In *Goeldiella eques, Cetopsorhamdia iheringi, Heptapterus mustelinus* and *Pimelodella gracilis,* the *medulla oblongata* is slightly bulged posterolaterally (Fig. 3). The length of the *medulla oblongata* in relation to the BL is similar in *R. quelen, G. eques* and *I. mirini,* although significantly different from the other examined species (Table 1).

The *lobus vagi* is located at the dorsal portion of the *rhombencephalon,* positioned beneath the supraoccipital and supraoccipital process (Fig. 1). In dorsal view, these lobes lie immediately posterior and continuous to the *lobus facialis* and are anteromedially located to the *medulla oblongata*. In all species examined the *lobus vagi* is composed of two cylindrical, paired, V-shaped lobes, with anterior bulges. These lobes contact each other only in their posterior portions, forming an acute tip (Figs. 2 and 3). The *lobus vagi* is longer than the *lobus facialis* in *R. quelen, G. eques* and *P. gracilis.* In all remaining species examined the inverse was found. The *lobus vagi* length in relation to BL is substantially smaller in *H. mustelinus* (Fig. 3, Table 1). The presence of a conspicuous bulge on the anterior portion of *lobus vagi* is shared by all Heptapteridae species examined herein (Fig. 3).

The *lobus facialis* is located at the dorsal portion of the *rhombencephalon,* positioned beneath the supraoccipital process (Fig. 1). In dorsal view, it is posterior to the *corpus cerebelli,* anterior to the *lobus vagi,* and medially located in relation to the lateral line lobe. A small portion of the anterior area of the *lobus facialis* is positioned beneath the posterior area of the *corpus cerebelli* (Fig. 2). The lobes of the *lobus facialis* are bilaterally symmetrical and do not contact each other. In all species examined these lobes are longitudinally elongate, somewhat rectangular-shaped, but with rounded edges in dorsal view. The *lobus facialis* is continuous with the *lobus vagi* and the lateral line lobe, but not with the *corpus cerebelli*. There is a conspicuous bulge laterally positioned over to each lobe of the *lobus facialis* (Figs. 2 and 3). Except for *H. mustelinus* and *P. gracilis,* the proportional length of the *lobus facialis* is larger than the length of the lateral line lobe in all species examined (Table 1). The length of the *lobus*

facialis in relation to BL is longer in *R. quelen, G. eques* and *I. mirini,* and shorter in *H. mustelinus* (Table 1).

The lateral line *lobe* is located at the dorsal portion of the *rhombencephalon* and is positioned beneath the supraoccipital (Fig. 1). It lies posterolateral to the *eminentia granularis* and the *corpus cerebelli* and is located laterally in relation to the *lobus facialis*. The lateral line lobe is formed by two conspicuous bulges, ovoid-shaped, with two subdivisions each one. The anterior bulge is located posterolaterally to the *eminentia granularis* and the

corpus cerebelli, while the posterior bulge is positioned lateral to the *lobus facialis.* In all examined species the anterior bulge is more prominent than the posterior bulge (Figs. 2, 3 and 4). In *R. quelen, G. eques* and *P. gracilis* the lateral line lobe extends up to the anterior portion of the *lobus vagi,* whereas in all remaining species these lobes extend up to the half-length of the *lobus facialis* (Figs. 2 and 3). In all examined species, the proportional width of the lateral line lobe is larger than to the *medulla oblongata* and smaller than the length of the *lobus vagi*
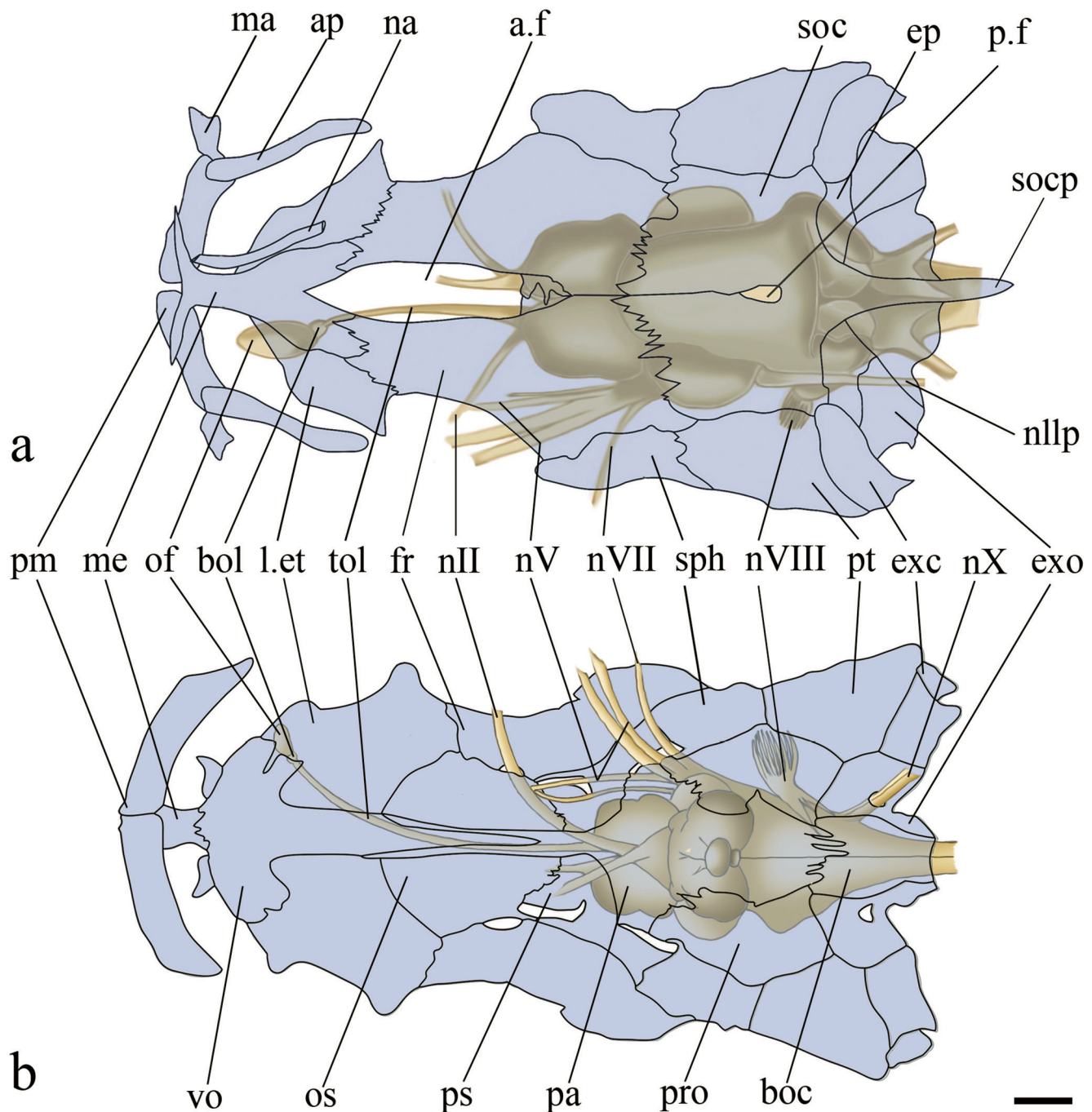

Figure 1. Camera lucida drawing of the brain and neurocranium of an adult specimen of *Rhamdia quelen,* MZUEL 7418, 64.03 mm SL, in dorsal (a) and ventral (b) views. a.f: anterior fontanel; ap: autopalatine; boc: basioccipital; bol: *bulbus olfactorius;* ep: epiotic; exc: extracapula; exo: exoccipital; fr: frontal; l.et: lateral ethmoid; ma: maxilla; me: mesethmoid; nll: *nervus opticus;* nV: *nervus trigeminus;* nVII: *nervus facialis;* nVIII: *nervus octavus;* nX: *nervus vagus;* na: nasal; nllp: *nervus lineae lateralis posterior;* of: olfactory organ; os: orbitosphenoid; pa: parasphenoid; p.f: posterior fontanel; p.m: premaxillary; pro: prootic; ps: pterosphenoid; pt: pterotic; soc: supraoccipital; socp: supraoccipital process; sph: sphenotic; tol: *tractus olfactorius;* vo: vomer. Scale bar = 1 mm.
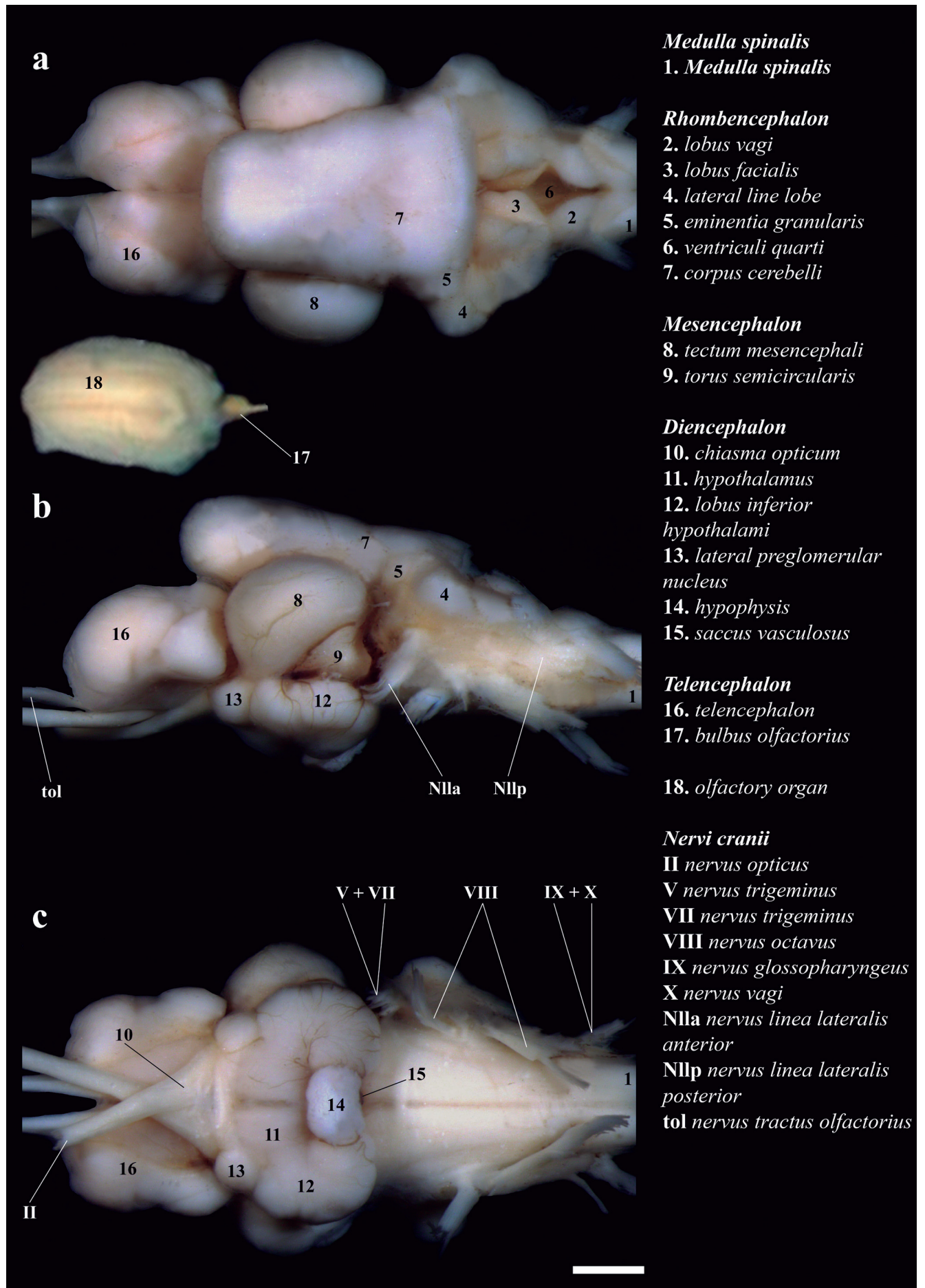
Medulla spinalis
1. ***Medulla spinalis***

Rhombencephalon
2. *lobus vagi*
3. *lobus facialis*
4. *lateral line lobe*
5. *eminentia granularis*
6. *ventriculi quarti*
7. *corpus cerebelli*

Mesencephalon
8. *tectum mesencephali*
9. *torus semicircularis*

Diencephalon
10. *chiasma opticum*
11. *hypothalamus*
12. *lobus inferior hypothalami*
13. *lateral preglomerular nucleus*
14. *hypophysis*
15. *saccus vasculosus*

Telencephalon
16. *telencephalon*
17. *bulbus olfactorius*

18. *olfactory organ*

Nervi cranii
II *nervus opticus*
V *nervus trigeminus*
VII *nervus trigeminus*
VIII *nervus octavus*
IX *nervus glossopharyngeus*
X *nervus vagi*
Nlla *nervus linea lateralis anterior*
Nllp *nervus linea lateralis posterior*
tol *nervus tractus olfactorius*

Figure 2. Brain of *Rhamdia quelen,* MZUEL 6036, 222.37 mm SL, in (a) dorsal, (b) lateral and (c) ventral views. Scale bar = 1 mm.

(Table 1). The width of the lateral line lobe relative to BL is similar in *R. quelen* and *G. eques.* The width of this lobe is larger in *P. gracilis,* and smaller in *H. mustelinus* and *I. mirini* (Table 1).

The *eminentia granularis* is located at the dorsal region of the *rhombencephalon,* positioned beneath the supraoccipital bone (Fig. 1). In dorsal and lateral views, it is posterolateral to the posterior area of the *corpus cerebelli,* anterior to the lateral line lobe, and posterior to the *tectum mesencephali.* The lobes of the *eminentia granularis* are somewhat cylindrical in dorsal view, and oval-shaped with the posterior portion slightly smaller than the anterior one, in lateral view. The *corpus cerebelli* is located at the dorsal portion of the *rhombencephalon,* positioned beneath the supraoccipital (Fig. 1). This lobe is located immediately anterior to the *lobus facialis,* dorsal to the *hypothalamus,* and medial to the lobes of the *tectum mesencephali.* The anterior portion of this structure is dorsal to the posterior area of the *telencephalon.* The *corpus cerebelli* has a trapezoid shape, with the anterior region slightly smaller than the posterior one. The dorsal margin in lateral view and the lateral margin in dorsal view are straight, without conspicuous undulations

(Fig. 2). In *R. quelen* and *P. gracilis* the anterior and posterior margins in dorsal view are also straight, whereas in *G. eques* the anterior portion is straight, and the posterior portion has two flaps (Fig. 3). In *H. mustelinus, I. mirini,* and *C. iheringi* the anterior portion of the *corpus cerebelli* is rounded, whereas the caudal portion is flap-shaped (Fig. 3). In *P. tenebrosa* the anterior portion is pointed and the posterior portion is flap-shaped (Fig. 3). The *corpus cerebelli* contacts the *telencephalon* in all examined species (Fig. 4). In all examined species the *corpus cerebelli* is the largest subdivision of the brain. The proportional length of the *corpus cerebelli* in relation to BL is longer in *H. mustelinus,* intermediate in *R. quelen* and *P. gracilis,* and shorter in *G. eques* and *I. mirini* (Table 1).

The efferent projections of the *nervus glossopharyngeus* and the *nervus vagus* emerge from the lateral wall of the *rhombencephalon,* approximately at half-length of the *lobus vagi.* These branches pass through the braincase by a foramen in the exoccipital. The *nervus octavus,* and *nervus linea lateralis posterior* emerge from the ventrolateral face of the *rhombencephalon,* at approximately the mid-point of the lateral line lobe. The *nervus facialis* and *nervus trigeminus* emerge from the ventrolateral wall
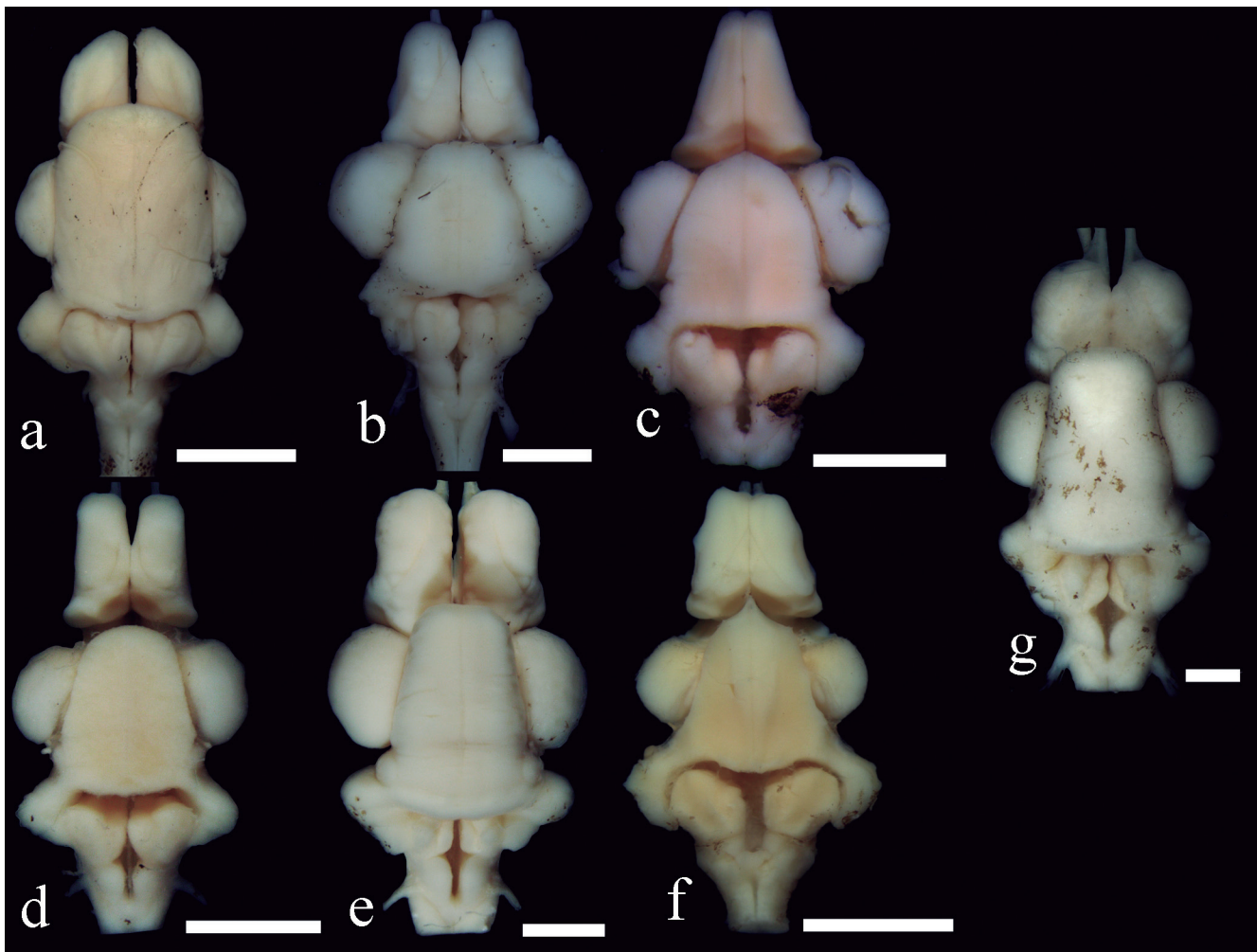

Figure 3. Brain of species of Heptapteridae in dorsal view. (a) *Cetopsorhamdia iheringi,* MZUEL 2260; (b) *Goeldiella eques,* MZUEL 7417; (c) *Heptapterus mustelinus,* MZUEL 5074; (d) *Imparfinis mirini,* MZUEL 4028; (e) *Pimelodella gracilis,* MZUEL 1574; (f) *Phenacorhamdia tenebrosa,* MZUEL 2706; (g) *Rhamdia quelen,* MZUEL 6036. Scale bar = 1 mm.

of the *rhombencephalon,* anterior to the *nervus octavus,* exiting the efferent projections of the braincase through a foramen on the suture between the parasphenoid, prootic and pterosphenoid. The anterior branches of the *nervus facialis* and *nervus trigeminus* exit their efferent projections from the braincase through a single foramen between the pterosphenoid, frontal and orbitosphenoid (Fig. 1).

Truncus cerebri

The *truncus cerebri* is located on the ventral surface of the brain; it is comprised by the *rhombencephalon* and the *mesencephalon.* It is positioned at the posterior portion of the *mesencephalon* to the anterior portion of the *medulla spinalis* (Fig. 2). Almost all cranial nerves exit their efferent projections from the *truncus cerebri,* except for the *nervus olfactorius* (nI) and the *nervus opticus* (nII). The cranial nerves that exit the *truncus cerebri* include: *nervus oculomotorius* (nIII), *nervus trochlearis* (nIV), *nervus trigeminus* (nV) *nervus abducens* (nVI), *nervus facialis* (nVII), *nervus octavus* (nVIII) *nervus glossopharyngeus* (nIX), *nervus vagus* (nX), *nervus lineae lateralis anterior* (nIIa) and the *nervus lineae lateralis posterior* (nIIp). Variations in the shape or proportional length of the *truncus cerebri* among the examined species were not found.
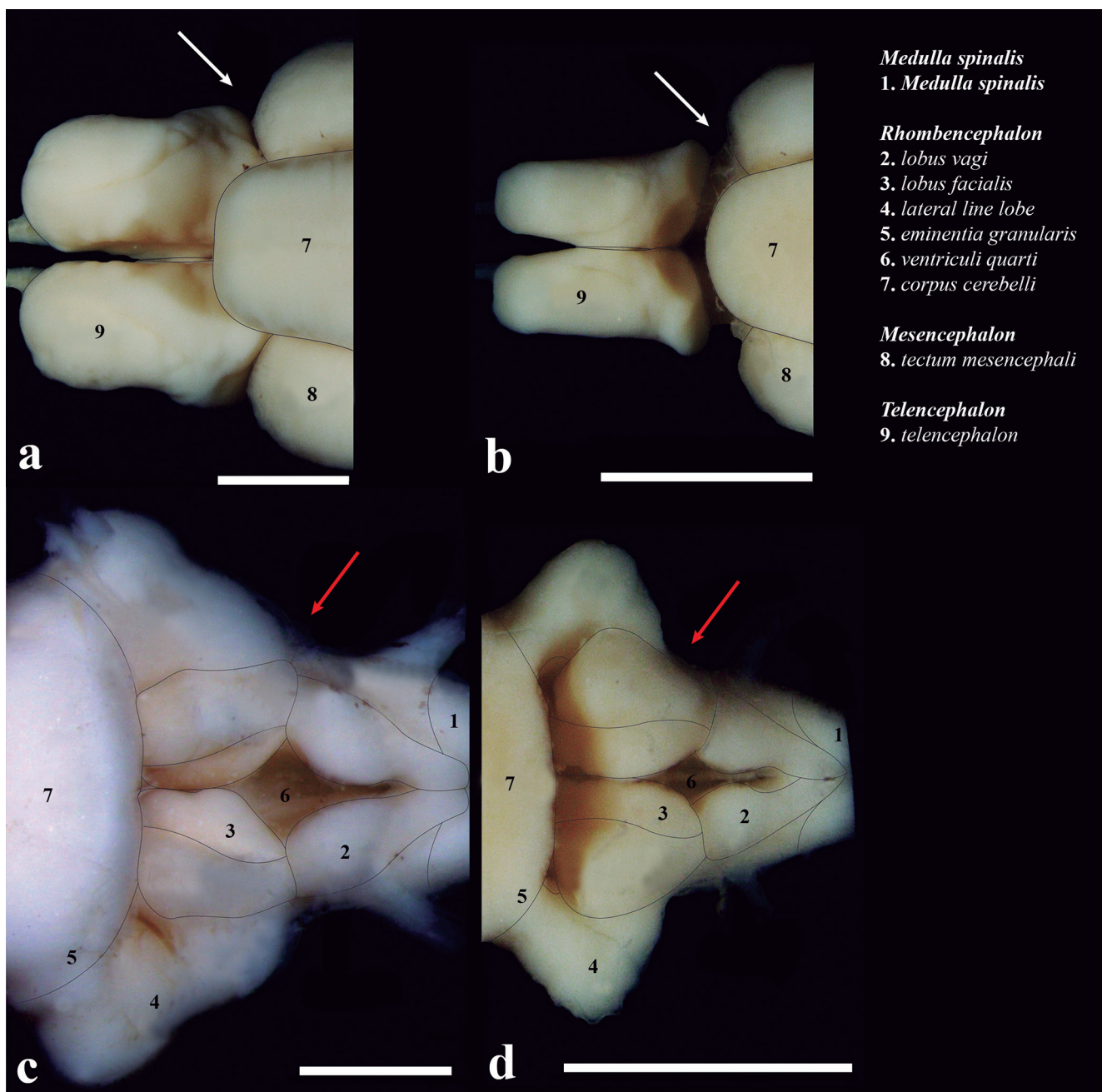

Figure 4. Details brain regions of species of Heptapteridae in dorsal view. (a) *Pimelodella gracilis,* MZUEL 1574; (b) *Imparfinis mirini,* MZUEL 4028; (c) *Rhamdia quelen,* MZUEL 6036; (d) *Imparfinis mirini,* MZUEL 4028. White arrows indicate the position of *tectum mesencephali* in relation to *telencephalon.* Red arrows indicate the position of lateral line lobe in relation to *lobus vagi.* Scale bar = 1 mm.

Mesencephalon

The *tectum mesencephali* is located at the dorsal portion of the *tegmentum mesencephalic,* lateral to the *corpus cerebelli* in dorsal view and posterior to the *telencephalon* in lateral view. The lobes of the *tectum mesencephali* are positioned beneath the supraoccipital and frontal bone (Fig. 1). This subdivision has two bilateral, almost spherical, lobes in dorsal and lateral views (Fig. 2). In *R. quelen, G. eques* and *P. gracilis* these lobes contact the *corpus cerebelli* and the *telencephalon.* In all remaining representatives, the *tectum mesencephali* contact only the *corpus cerebelli* (Fig. 3). In all specimens, the length of the *tectum mesencephali* is proportional shorter than the length of the *corpus cerebelli, telencephalon,* and the *lobus inferior hypothalami* (Table 1). The length of the *tectum mesencephali* in relation to BL is substantially shorter in *I. mirini* (Table 1).

The *nervus opticus* (nII) emerges from the *tectum mesencephali* on the *mesencephalon,* and its efferent projections exit in the region immediately anterior to the *lobus inferior hypothalamic.* These fibers contact each other and cross the midline of the brain at the region of the *chiasma mesencephalic.* The efferent projections of the *nervus opticus* exit the braincase through a foramen located between the frontal and orbitosphenoid, near the pterosphenoid (Fig. 1).

Diencephalon

The *lobus inferior hypothalami* is located at the ventral portion of the *diencephalon,* in a posterior region to the *chiasma mesencephali,* ventral to the *truncus cerebri* and the *tectum mesencephalic,* lateral to the *hypothalamus* in ventral view, and posterior to the *telencephalon* in lateral view (Fig. 2). The lobes of the *lobus inferior hypothalami* are positioned above the parasphenoid and prootic (Fig. 1). The *lobus inferior hypothalami* is semicircular, with the anterior portion slightly smaller than the posterior portion. The *hypophysis* remains anchored posteriorly on the *lobus hypothalamus* and is located between the lobes of the *lobus inferior hypothalami* (Fig. 2). The *hypothalamus* is also located at the ventral portion of the *diencephalon,* medially and above the *lobus inferior hypothalamic.* The lobes of the *hypothalamus* are rounded. The proportional length of the *lobus inferior hypothalami* is shorter than the *telencephalon* only in *R. quelen, G. eques* and *H. mustelinus* (Table 1). The length of this subdivision in relation to BL is longer in *H. mustelinus* (Table 1).

Telencephalon

In all examined specimens, the *telencephalon* is located anterior to the *tectum mesencephali* in lateral view, posterior to the *bulbus olfactorius,* and with the posterior area positioned beneath the *corpus cerebelli* in dorsal and lateral views (Fig. 2). The lobes of the *telencephalon* are positioned completely beneath the frontal (Fig. 1). In *I. mirini* the *telencephalon* does not contact the *corpus cerebelli* (Fig. 3). The *telencephalon* is longitudinally elongate, like a cylinder, with both the anterior and posterior margins rounded. In all examined species the anterior margin of the *telencephalon* is slightly smaller than the posterior one. In *R. quelen* and *P. gracilis* the anterior and posterior margins of these lobes have equivalent widths. In all remaining examined species the anterior portion is slight smaller than the posterior one (Fig. 3). There are no substantial differences in the proportional length of this subdivision among species examined (Table 1).

The *bulbus olfactorius* is stalked and is positioned at the anterior portion of the brain. This structure is located beneath the nasal, near to the articulation between the lateral ethmoid and the vomer (Fig. 1). The *bulbus olfactorius* is rounded, with equivalent widths of its anterior and posterior margins. It is connected to the olfactory epithelium via the *nervus olfactorius,* and to the *telencephalon* via the *tractus olfactorius* (Fig. 2). Length and shape variations of the *bulbus olfactorius* were not found. The olfactory epithelium is rounded, with the anterior margin slight smaller than the posterior one. It has a considerable amount of lamellae on each side, granting it a feather appearance (Fig. 2).

DISCUSSION

Morphometric and gross morphology variations were found on the brains of the examined species. No minor intraspecific variation and sexual dimorphism in brains were observed. These combinations of remarkable intergeneric and limited intraspecific variations suggest that characters derived from brain anatomy may be useful for phylogenetic inferences.

The brain gross morphology of *R. quelen* and other species of the Heptapteridae examined here share some features with other members of the Pimelodoidea, a clade corroborated by morphological (Lundberg *et al.,* 1991; Bockmann, 1998; Bockmann & Guazzelli 2003; Lundberg & Littmann, 2003; Shibatta, 2003; Birindelli & Shibatta, 2011) and molecular-based data (Hardman, 2005; Sullivan *et al.,* 2006; Sullivan *et al.,* 2013). These shared conditions and characters are: (1) the *lobus vagi* composed of two cylindrical, paired, and V-shaped lobes, and (2) the lateral line lobe composed of two conspicuous bulges, ovoid-shaped, with the anterior portion more prominent than the posterior one. Contrasting to Pimelodidae and Pseudopimelodidae, members of the Heptapteridae share the following putative synapomorphies: (1) the position of the *hypophysis* at the posterior area of the *hypothalamus* (*vs.* anchored at the midpoint of the *hypothalamus*) and (2) the presence of lateral subdivision on the *lobus facialis* (*vs.* anterolateral positioned).

According to brain gross morphology of *R. quelen* and other examined species of Heptapteridae, a spectrum of variation is notable where at one end are located the genera *Rhamdia, Pimelodella* and *Goeldiella,* and on the other all the remaining heptapterids examined herein. While the first three taxa exhibit the *telencephalon* with a tumid anterior area, along the relative smaller length of the *lobus facialis,* all other Heptapteridae taxa have

the *telencephalon* with thinner anterior area, along the relative longer length of the *lobus facialis.* The proportional length of the *lobus vagi* longer than the *lobus facialis,* the lateral line lobe extending up to the anterior portion of the *lobus vagi,* and the *tectum mesencephali* contacting the *corpus cerebelli* and the general shape of the *telencephalon* are features present in *R. quelen, P. gracilis* and *G. eques.* The widths of the anterior and posterior portions of the *telencephalon* and their proportional length, and the straight posterior portion of the *corpus cerebelli* are complementary features present in *R. quelen* and *P. gracilis* (Fig. 3 and Table 1). Based on morphological and osteological features, Bockmann (1998) proposed that the genus *Goeldiella* was sister group of all other heptapterids, however there is no consensus on *Rhamdia* and *Pimelodella* position. The phylogenetic relationship at the base of Heptapteridae cladogram remain uncertain (Bockmann & Miquelarena, 2008; Slobodian & Bockmann, 2013). Future comprehensive research on Pimelodoidea neuroanatomy may contribute to elucidate those assumptions.

The length of the *lobus facialis* proportionally greater than length of the *lobus vagi,* the lateral line lobe extending up to the half-length of the *lobus facialis,* the *tectum mesencephali* not contacting the *telencephalon,* and the shape of the posterior and anterior portions of the *telencephalon,* are all traits found in *Cetopsorhamdia iheringi, Heptapterus mustelinus, Imparfinis mirini,* and *Phenacorhamdia tenebrosa* (Fig. 3; Table 1). This separation agrees with the proposal of Ferraris Jr. (1988) and Bockmann (1994) who included *Cetopsorhamdia, Heptapterus, Imparfinis* and *Phenacorhamdia,* in the *Nemuroglanis* sub-clade, as a distinct group within heptapterids.

The shape, position, and proportional lengths of the brain as a whole, and its different subdivisions, corroborate the relationship hypothesis using external morphology and osteological characters presented by Ferraris Jr. (1988) and Bockmann (1998). These brain characters may allow recognition and resolution of smaller lineages within the family if incorporated to a broader phylogenetic reconstruction of the group.

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