Received: 24 February 2021 | Revised: 1 April 2021 | Accepted: 2 April 2021

DOI: 10.1002/cne.25152

COMMENTARY

JCN RESEARCH IN SYSTEMS NEUROSCIENCE THE JOURNAL OF COMPARATIVE NEUROLOGY WILEY

Mushroom bodies and reniform bodies coexisting in crabs cannot both be homologs of the insect mushroom body

Nicholas J. Strausfeld

Department of Neuroscience, University of Arizona, Tucson, Arizona, USA

Correspondence
Nicholas J. Strausfeld, Department of Neuroscience, University of Arizona, Tucson, AZ.
Email: flybrain@email.arizona.edu

Funding information
National Science Foundation, Grant/Award Number: 1754798

Abstract

In one species of shore crab (Brachyura, Varunidae), a center that supports long-term visual habituation and that matches the reniform body's morphology has been claimed as a homolog of the insect mushroom body despite lacking traits that define it as such. The discovery in a related species of shore crab of a mushroom body possessing those defining traits renders that interpretation unsound. Two phenotypically distinct, coexisting centers cannot both be homologs of the insect mushroom body. The present commentary outlines the history of research leading to misidentification of the reniform body as a mushroom body. One conclusion is that if both centers support learning and memory, this would be viewed as a novel and fascinating attribute of the pancrustacean brain.

KEYWORDS
divergence, homology, misidentification, mushroom body, phenotype, reniform body

1 | INTRODUCTION

Bellonci's studies of the stomatopod crustacean *Squilla mantis* identified a center in the brain that he claimed as identical to the insect mushroom body, referring to criteria already determined by Dietl (1876) and Berger (1878) for identifying such centers in insects. Bellonci also discovered a second prominent neuropil that was unambiguously distinct from the first. His description, translated from the Italian original, is clear: "Another body formed of dense and very fine reticulated substance .... is somewhat smaller than the hemiellipsoidal body (Bellonci's name for the mushroom body calyx) and has the shape of a kidney; therefore, I call it the reniform body." He could find no evidence of connections between the two centers. His view was that the mushroom body and reniform body are morphological distinct.

It is now recognized that a unique arrangement of 13 traits defines the mushroom body of a stomatopod as explicitly as one in an insect (Wolff et al., 2017). This "canonical" mushroom body has become the morphological yardstick for assessing putative phenotypic homologs that occur across Eumalacostraca (Strausfeld et al., 2020). Confidence in this yardstick makes it possible to recognize even radical departures from the ground pattern and to detect possible misidentifications (Strausfeld & Sayre, 2021). A recent example of misidentification is exemplified by two papers claiming that in a species of Brachyura (crabs) the reniform body, as recognized in Stomatopoda, is homologous to the insect mushroom body (see, Maza et al., 2020; Maza, Sztarker, et al., 2016).

2 | THE RENIFORM BODY DOES NOT CORRESPOND TO THE CANONICAL MUSHROOM BODY

Reniform bodies and mushroom bodies are each defined by their own distinctive set of morphological traits (Table 1), those of reniform bodies identified from observations of Stomatopoda and the crab *Hemigrapsus nudus* (Thoen et al., 2020). Some of those traits are indeed recognized by Maza et al. (2020) but interpreted as belonging to an insect-like mushroom body. Invariant features of the reniform body morphology that might be mistaken for mushroom body traits include a dense group of quite small perikarya, numbering in the hundreds, situated on the dorsal surface of the lateral protocerebrum. These provide smooth axons collected as a tight bundle, called the pedestal, extending toward the lateral protocerebrum's ventral surface (Thoen et al., 2020). At about midway, the pedestal branches to provide an approximately parallel collateral bundle, from which arise two

TABLE 1 Traits pertaining to mushroom bodies and reniform bodies

	Trait	Identity: Mushroom body	Identity: Reinform body
1	Brain's smallest neuronal perikarya clustered dorsally or laterally at the rostral surface of the lateral protocerebrum	Globuli cells	
2	Dense distal synaptic neuropil providing columnar extension(s) (#8)	Calyx	
3	Small neuronal perikarya clustered anteriorly, adjacent to lobula		Reinform cell body cluster
4	Tightly grouped axons lacking synaptic specialization originating from perikaryal cluster (#3) extending across the lateral protocerebrum		Pedestal
5	Parallel grouped axon bundle from the perikaryal cluster (#3)		Collateral tributary
6	Voluminous branching arbors parsed into four to five discrete territories		Zones (iz, lz, dz, pz, mz)
7	Axons smooth, lacking specializations indicative of synaptic sites		Pedestal
8	Approximately parallel, sometimes net-like ensembles of axon-like processes	Columns	
9	Ensembles (#8) morphologically distinct	Columns	
10	Spinous and varicose specializations in ensembles (#8) indicative of preynaptic and postsynaptic sites	Columns	
11	Approximately orthogonally arranged networks	Columns and calyces	
12	Synaptic territories defined by basket, spinous, or claw-like specializations	Calyces	Zones (iz, lz, mz, dz, pz)
13	Territories denoted by diffuse anti-TH, anti-5HT, or anti-GAD immunoreactive processes		Zones (lz, mz, dz, pz)
14	Elevated expression of anti-DC0 immunoreactivity	All components	All components
15	Parallel ensembles of processes (8) can provide terminal tubercles	Columns	
16	Distal neuropil comprises discrete dendritic domains and strata	Calyces	
17	Distal neuropil comprises uniform arborizations		Intial zone
18	Anti-GAD immunoreactive recurrent pathways and/or local systems	Calyces	
19	Anti-TH, anti-5HT and anti-GAD immunoreactive arborizations intersect and partition columnar ensembles	Columns	
20	Anti-TH, anti-5HT, and anti-GAD immunoreactive efferent and afferent fields define local domains	Calyces	

Note: Two traits (12, 14) are shared by both centers. Seven traits pertain to reniform bodies, previously described in the study by Wolff et al. (2017), Strausfeld et al. (2020), and Thoen et al. (2020). Thirteen traits pertaining to the canonical mushroom body, originally identified in the mushroom bodies of Stomatopoda, *Drosophila* and *Periplaneta*, are described and illustrated in the study by Wolff et al. (2017); see: https://elifesciences.org/articles/29889/figures#fig1s1).

to three dense systems of profusely branching processes that extend proximally. These define the reniform body's proximal and medial domains of dense arborizations (Figure 1). The pedestal gives rise to two more domains extending toward the optic lobe, the distal and lateral zones (Figure 1). A field of processes (called the initial zone; Wolff et al., 2017) extends bilaterally from the pedestal immediately beneath its origin from its cluster of perikarya (Figure 1; see also figure 2 in the study by Thoen et al., 2020). As demonstrated in the stomatopod *Neogonodactylus oerstedii*, the reniform body's domains are distinguished by their signature immunoreactivities to antibodies raised against serotonin and glutamate decarboxylase (GAD; Wolff et al., 2017). The domains also differ with regard to their afferent supply and the morphologies of their dendritic baskets and glomeruli, which are much larger than those of a mushroom body's calyces (see figure 5 in the study by Thoen et al., 2020). Belying Bellonci's opinion, dye application to the reniform body demonstrates interneurons connecting it to the mushroom body calyces and to its column (figures 4 and 8 in the study by Thoen et al., 2020).

Among features unambiguously differentiating the reniform body and mushroom body is the fibrous composition of their elongated extensions, the pedestal and the column, respectively. The reniform body's pedestal is an axonal tract: its fibers are strictly parallel, densely packed, and devoid of any specializations that would indicate synaptic sites. This contrasts with the mushroom body's columns, which comprise systems of processes belonging to intrinsic neurons. The many calycal dendrites of intrinsic neurons provide processes that are only approximately parallel but are richly equipped with specializations indicative of presynaptic and postsynaptic sites. Antibodies against serotonin (5HT) and tyrosine hydroxylase (TH) demonstrate that arborizations that are immunoreactive to these antisera intersect the processes of intrinsic neurons and partition the mushroom body column into discrete domains (Wolff et al., 2017). Antibodies against 5HT and TH reveal no arborizations in the reniform body pedestal,

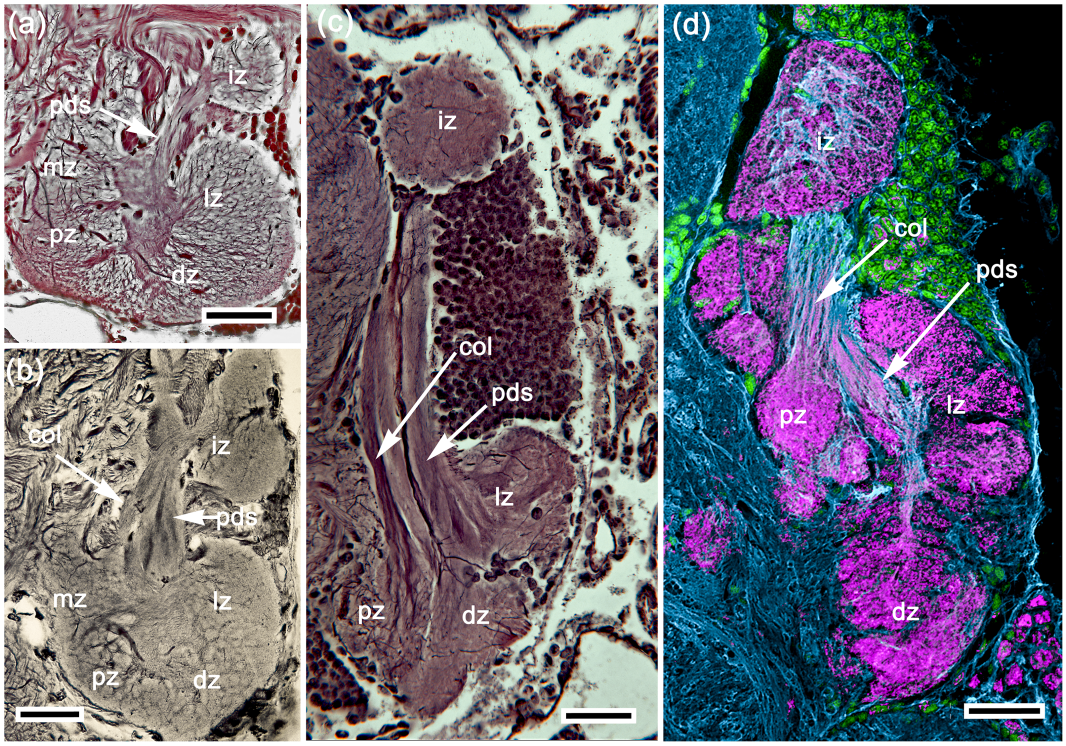

FIGURE 1 Reniform bodies show little neuroanatomical divergence. (a) The reniform body of the stomatopod *Gonodactylus chiragra* comprises five domains, called the initial (iz), lateral (lz), distal (dz), proximal (pz), and medial (mz) zones, all extending from a columnar pedestal (pds). (b) The reniform body of the banded coral shrimp *Stenopus hispidus*, showing the same organization. The pedestal is here resolved with its parallel collateral (col). (c, d) Even in the highly modified brains of Alpheidae, which have reduced optic lobes, the elongated reniform bodies of the visored shrimp *Betaeus harrimani* (c) and the pistol shrimp *Alpheus bellulus* (d) show homologous arrangements of parts. (Scale bars: (a) 100 μm; (b–d) 50 μm; (panel a, from the study by Thoen et al., 2020; panels c, d, from the study by Strausfeld et al., 2020)

but they do demonstrate immunoreactive processes outside the pedestal (Figure 2(e–g)). However, irrespective of these differences (Table 1), mushroom bodies and reniform bodies do share two traits (Strausfeld et al., 2020; Thoen et al., 2020). One refers to synaptic specializations, albeit in dissimilar components (mushroom body calyces, reniform body zones). The other is their strong immunoreactivity to antibodies raised against DC0, the catalytic subunit of protein kinase A, encoded by the *Drosophila* gene DC0 (Kalderon & Rubin, 1988). DC0 is required for learning and memory in *Drosophila* (Skoulakis et al., 1993), hence its utility in resolving putative centers that support learning and memory (Farris, 2005; Wolff & Strausfeld, 2015). In addition to revealing mushroom bodies, anti-DC0 selectively labels the ellipsoid body, a center situated at the protocerebrum's midline (Thoen et al., 2017; Wolff et al., 2012). In *Drosophila*, the ellipsoid body is required for visual working memory (Kuntz et al., 2012).

3 | RENIFORM BODIES ARE HIGHLY CONSERVED, MUSHROOM BODIES DIVERGE

Whereas mushroom bodies of Stomatopoda and "shrimps" (Stenopodidea and Caridea) show lineage-specific phenotypic divergences (Sayre & Strausfeld, 2019; Strausfeld et al., 2020), their reniform bodies are denoted by their evolutionarily stable morphology. Problems of identity are, however, presented by Reptantia, a natural group that is united by a novel component of the olfactory system called the accessory lobe (Sandeman et al., 1993; Wolfe et al., 2019). Reptantians, except Brachyura, have greatly reduced reniform bodies or appear to have lost them entirely. Mushroom bodies in Achelata (spiny lobsters), Axiidea (mud shrimps), and Astacidea (crayfish, true lobsters) have undergone radical modification: the reduction and integration of the column into large bipartite calyces (Sayre & Strausfeld, 2019). In Anomura (hermit crabs and squat lobsters), mushroom bodies are multistratified dome-like neuropils, usually lacking columns (Strausfeld & Sayre, 2020; Wolff et al., 2012). Nevertheless, the same traits as those defining the canonical columnar mushroom body also define those highly divergent neuropils (Strausfeld et al., 2020). Until recently, no mushroom body had been identified by those traits in Brachyura, whereas Varunidae (shore crabs) have been demonstrated to possess prominent reniform bodies (Strausfeld et al., 2020; Thoen et al., 2020; Wolff et al., 2017), as do Ocypodidae (fiddler crabs), both compared here in Figure 2(c,d). Their morphology and location conform to reniform bodies identified in Stomatopoda, Stenopodidea, and Caridea (Figures 1 and 2;

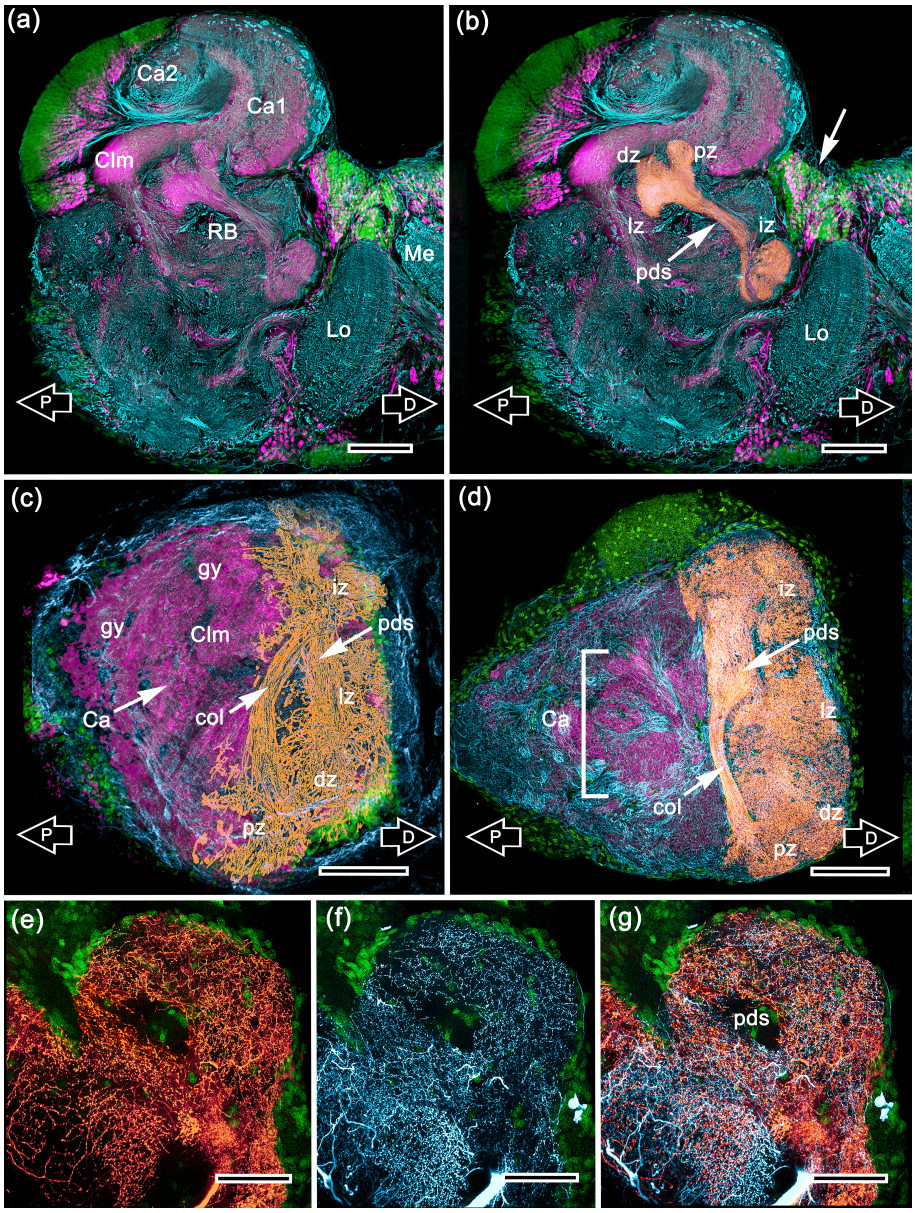

FIGURE 2 Conserved neural morphologies of reniform bodies contrast with mushroom body divergences. (a, b) Lateral view of the lateral protocerebrum of the thorid shrimp *Lebbeus groenlandicus* (P indicates proximal, toward midbrain; D indicates distal, toward compound eye). Its two contiguous calyces (Ca1, Ca2) both provide columns (only that of Ca1 shown, Clm). The reniform body (RB) extends across the distal part of the lateral protocerebrum. False colors (panel b) emphasize its division into four zones (iz initial zone, lz lateral zone, dz dorsal zone, pz proximal zone), each extending from the pedestal (pds), which is supplied by anti-DC0 immunoreactive perikarya lying immediately above the initial zone (arrowed in panel b). (c, d) The reniform body, enhanced by false coloration, in two Brachyura species, the shore crab *Hemigrapsus nudus* (c) and the fiddler crab *Uca minax* (d), lies immediately distal to the mushroom body and its gyri (shown in magenta). Both are viewed looking downward through the rostral surface of the lateral protocerebrum. (e–g) Unlike mushroom bodies, where the arborizations of anti-TH and anti-5HT immunoreactive neurons define discrete fields intersecting its columns, in reniform bodies immunoreactive neurons branch outside the pedestal in specific zones, here shown in the lateral zone in *Uca minax*. Anti-5HT immunoreactivity is orange, anti-tyrosine hydroxylase (TH) immunoreactivity is cyan. The merged images (g) demonstrate the preponderance of 5HT, compared with TH, associated with the RB. Lo, lobula; Me, medulla; gy, gyri; col, collateral. Scale bars: (a, b), 200 μm; (c, d), 100 μm; (e–g), 50 μm

also Strausfeld et al., 2020; Thoen et al., 2020). However, an earlier body of research on learned visual behaviors by the shore crab *Chasmagnathus granulatus* (now *Neohelice granulata*) has led to the interpretation of the brachyuran reniform body as a mushroom body (Maza, Sztarker, et al., 2016). The following provides a very brief digest of research leading to this misidentification.

4 | VISUAL HABITUATION, THE RENIFORM BODY, AND ITS MISINTERPETATION AS A MUSHROOM BODY

Research initiated in 1988 by Héctor Maldonado at the Universidad de Buenos Aires (see Lozada et al., 1990; Maldonado, 2002) on the effects of opioids on learning by the shore crab (Brunner & Maldonado, 1988; Tomsic et al., 1993) progressed to identifying neural correlates of long-term habituation evoked by repetitive visual stimuli (see Hemmi & Tomsic, 2012; Tomsic & Romano, 2013). An important advance was the identification of not only visual neurons associated with escape response plasticity (Medan et al., 2007; Sztarker and Tomsic, 2008) but also ensembles of candidate neurons that suggested which pathways likely mediate habituation (Berón de Astrada et al., 2013). Subsequent optical recordings detecting such activity (Maza, Locatelli, & Delorenzi, 2016) demonstrated it to be associated with a group of well-defined neuropils. Thus, as shown in insects (Ayse et al., 2019), visual associative learning and memory are not restricted to just mushroom bodies but involve dynamic modification of the optic lobes and other associated centers. Nevertheless, despite being neuroanatomically distinct from mushroom bodies, neuropils in the crab supporting long-term visual habituation, a form of learning, were claimed to correspond to the vertical and medial lobes of insect mushroom bodies (Maza, Sztarker, et al., 2016). However, it is precisely that neuropil described by Maza, Sztarker, et al. (2016) that corresponds not to a mushroom body but to the distinctive morphology of the reniform body, as described from the stomatopod *Neogonodactylus oerstedii* and the brachyuran *Hemigrapsus nudus* (Thoen et al., 2020). A further complication is that a redescription of the center (Maza et al., 2020) declares it homologous with the decapod "hemiellipsoid body," a nomenclature, introduced by Bellonci (1882) to exclusively denote the mushroom body calyces. The term has consistently been misunderstood for well over a century (Strausfeld, 2020), and at most might once have suited mushroom bodies lacking columns, as in Achelata, Astacidea, and Axiidea (Strausfeld et al., 2020; Strausfeld & Sayre, 2020).

5 | EXPRESSIO UNIUS, EXCLUSIO ALTERIUS

It is understandable that a neuropil comprising a pedunculus-like column and providing discrete volumes of processes could pass muster as a mushroom body homolog in the absence of any other candidate in the crab. Indeed, this likely contributed to the reniform body originally being accorded a mushroom body identity in 2016 (Maza, Sztarker, et al., 2016), before the first modern description of the reniform body (Wolff et al., 2017). However, that misinterpretation has persisted (Maza et al., 2020), even though anti-DC0 immunostaining of the crab's lateral protocerebrum suggested that areas of its neuropil, to which the reniform body is adjacent, represent a modified mushroom body (Strausfeld et al., 2020; Thoen et al., 2020).

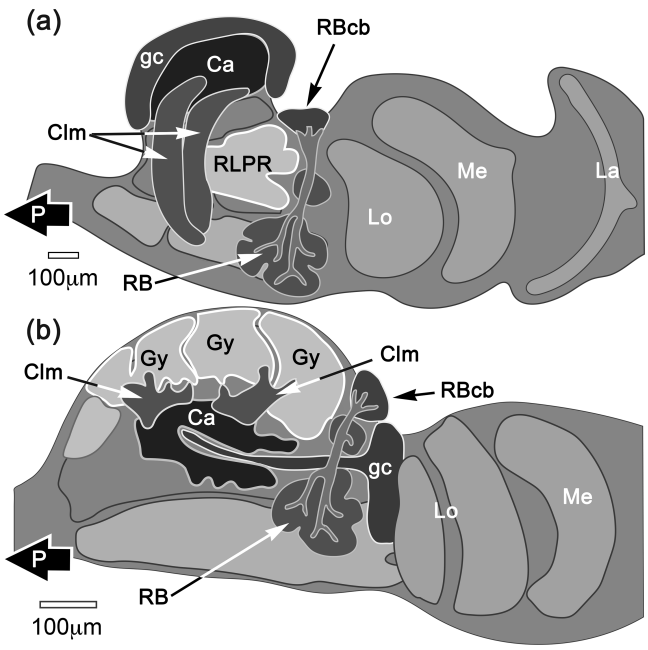

FIGURE 3 Morphological distinctions of the stomatopod and varunid mushroom bodies contrast with conserved arrangements of their reniform bodies. (a) As illustrated by Stomatopoda, the calyces (Ca) of pancrustacean mushroom bodies surmount the rostral surface of the lateral protocerebrum, with their columns (Clm) extending caudally into it. Globuli cells (gc), which supply the columns, lie above or medial to the calyces. Outputs from the columns extend to the midbrain (not shown), others supply destinations in the rostral volume of the lateral protocerebrum (RLPR). (b) In the shore crab *Hemigrapsus nudus* (and the fiddler crab *Uca minax*), the mushroom body is inverted, and its calyces (Ca) are buried within the rostral part of the lateral protocerebrum. The mushroom body's columns reach outwards to a system of gyri (Gy) covering the rostral surface. The calyces are supplied by globuli cells situated immediately proximal to the lobula (Lo). Notably, the disposition and components of the reniform bodies (RB) and their clusters of cell bodies (RBcb) are the same in both taxa, attesting to the morphological constancy of this center (see also Strausfeld & Sayre, 2021). P (in arrow), proximal, toward the midbrain; La, lamina; M, medulla; Lo, lobula

A recent study has verified that those areas of immunoreactive neuropil indeed belong to a substantial mushroom body (Strausfeld & Sayre, 2021). However, in the shore crab *Hemigrapsus nudus*, the mushroom body calyces are not disposed at the rostral surface of the lateral protocerebrum, as they are in other eumalacostracans. Instead, the entire mushroom body is cryptic; its calyces are buried deep within the lateral protocerebrum's rostral volume. Instead of columns extending caudally into the underlying neuropils, as shown schematically in Figure 3(a), mushroom body columns in *H. nudus* extend rostrally to a system of gyri at the protocerebrum's surface (Figure 3(b)). It is those strongly anti-DC0-immunoreactive gyri that obscure the immunoreactive calyces and columns (Strausfeld & Sayre, 2021).

Traits defining the canonical mushroom body (Table 1) are consistent with those comprising the inverted varunid mushroom body (Strausfeld & Sayre, 2021). But they do not apply to the reniform body

(Table 1). In the crab, as in Stomatopoda, Stenopodidea, and Caridea, the mushroom body and the reniform body occur together but are separate and distinct. The reniform body is always disposed between the mushroom body and the optic lobe (Figures 2(b) and 3(a,b)), which is the arrangement originally described by Bellonci (1882).

Studies of the crayfish mushroom body define it as a multisensory integrator (Mellon, 2000). Context-dependent visual habituation by the reniform body (Maza, Sztarker, et al., 2016) thus identifies a second specialized neuropil in eumalacostracans serving multisensory convergence and, in addition, habituation. If confirmed that both centers support long-term memory, this would be a major finding. That the reniform body provides direct connections to the mushroom body (Thoen et al., 2020) allows speculation that mushroom body sensory association circuits, or outputs from them, may be subject to modulation by afferents from the reniform body encoding states of visual awareness.

The identification of a mushroom body in the crab returns us to Patterson's (1988) dictum that claiming as homologous two phenotypically distinct structures in the same organism fails the homology criteria of similarity, congruence, and conjunction. Thus, the reniform body, which lacks most of the traits that define a mushroom body, cannot be given the identity of a mushroom when it accompanies a center comprising the full complement of traits that do define a mushroom body. This dismisses the claims of Maza, Sztarker, et al. (2016) and Maza et al. (2020). Rather, the coexistence of the mushroom body and reniform body aligns organization in the varunid brain with the brains of those taxa that also possess both centers.

ACKOWLEDGMENTS

Immunohistological data for this account were generated with Marcel E. Sayre (Lunds Universitet, Sweden), with support from the U.S. National Science Foundation grant no. 1754798. The author thanks Sarah Farris (West Virginia University), Pedro Martínez (Universitat de Barcelona), and Charles Derby (Georgia State University), and an anonymous reviewer for their valuable suggestions. The author is, as always, indebted to Camilla Strausfeld for discussions, sage advice, and expert editing that has resulted in the final version of this work. This study was supported by the U.S. National Science Foundation grant no. 1754798.

CONFLICT OF INTEREST

The author has no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1002/cne.25152.

DATA AVAILABILITY STATEMENT

DATA AVAILABILITY STATEMENT Histological material contributing to this commentary piece is curated at the author's laboratory in the University of Arizona's Department of Neuroscience.

ORCID

Nicholas J. Strausfeld https://orcid.org/0000-0002-1115-1774

REFERENCES

Ayse, Y., Grübel, K., Spaethe, J., & Rössler, W. (2019). Distributed plasticity in ant visual pathways following colour learning. *Proceedings of the Royal Society B*, *286*, 20182813. http://doi.org/10.1098/rspb.2018.2813

Bellonci, G. (1882). Nuove ricerche sulla struttura del ganglio ottico della *Squilla mantis*. *Memorie della Accademia delle Scienze dell'Istituto di Bologna*, *4*, 419–426.

Berger, E. (1878). Untersuchungen über den Bau des Gehirns und der Retina der Arthropoden. *Arbeiten aus dem Zoologischen Instituten der Universität Wien und der Zoologischen Station in Triest*, *1*(2), 1–48.

Berón de Astrada, M., Bengochea, M., Sztarker, J., Delorenzi, A., & Tomsic, D. (2013). Behaviorally related neural plasticity in the arthropod optic lobes. *Current Biology*, *23*, 1389–1398. https://doi.org/10.1016/j.cub.2013.05.061

Brunner, D., & Maldonado, H. (1988). Habituation in the crab *Chasmagnathus granulatus*: Effect of morphine and naloxone. *Journal of Comparative Physiology A*, *162*, 687–694. https://doi.org/10.1007/BF01342643

Dietl, M. J. (1876). Die Organisation des Arthropodengehirns. *Zeitschrift für Wissenschaftliche Zoologie*, *27*, 488–517.

Farris, S. M. (2005). Evolution of insect mushroom bodies: Old clues, new insights. *Arthropod Structure & Development*, *34*, 211–234. https://doi.org/10.1016/j.asd.2005.01.008

Hemmi, J. M., & Tomsic, D. (2012). The neuroethology of escape in crabs: From sensory ecology to neurons and back. *Current Opinion in Neurobiology*, *22*, 194–200. https://doi.org/10.1016/j.conb.2011.11.012

Kalderon, D., & Rubin, G. M. (1988). Isolation and characterization of *Drosophila* cAMP-dependent protein kinase genes. *Genes & Development*, *2*, 1539–1556. https://doi.org/10.1101/gad.2.12a.1539

Kuntz, S., Poeck, B., Sokolowski, M., & Strauss, R. (2012). The visual orientation memory of *Drosophila* requires foraging (pkg) upstream of ignorant (rsk2) in ring neurons of the central complex. *Learning and Memory*, *19*, 337–340.

Lozada, M., Romano, A., & Maldonado, H. (1990). Long-term habituation to a danger stimulus in the crab *Chasmagnathus granulatus*. *Physiology & Behavior*, *47*, 35–41.

Maldonado, H. (2002). Crustaceans as models to investigate memory illustrated by extensive behavioral and physiological studies in *Chasmagnathus*. In K. Wiese (Ed.), *The crustacean nervous system* (pp. 314–327). Springer. https://doi.org/10.1007/978-3-662-04843-6_24

Maza, F. J., Locatelli, F. F., & Delorenzi, A. (2016). Neural correlates of expression-independent memories in the crab *Neohelice*. *Neurobiology of Learning and Memory*, *131*, 61–75. https://doi.org/10.1016/j.nlm.2016.03.011

Maza, F. J., Sztarker, J., Cozzarin, M. E., Lepore, M. G., & Delorenzi, A. (2020). A crab's high-order brain center resolved as a mushroom body-like structure. *Journal of Comparative Neurology*, *529*, 501–523. https://doi.org/10.1002/cne.24960

Maza, F. J., Sztarker, J., Shkedy, A., Peszano, V. N., Locatelli, F. F., & Delorenzi, A. (2016). Context-dependent memory traces in the crab's mushroom bodies: Functional support for a common origin of high order memory centers. *Proceedings of the National Academy of Science of the United States of America*, *113*, E7957–E7965. https://doi.org/10.1073/pnas.1612418113

Medan, V., Oliva, D., & Tomsic, D. (2007). Characterization of lobula giant neurons responsive to visual stimuli that elicit escape behaviors in the crab *Chasmagnathus*. *Journal of Neurophysiology*, *98*, 2414–2428. https://doi.org/10.1152/jn.00803.2007

Mellon, D. F. (2000). Convergence of multimodal sensory input onto higher-level neurons of the crayfish olfactory pathway. *Journal of Neurophysiology*, *84*, 3045–3055. https://doi.org/10.1152/jn.2000.84.6.3043

Patterson, C. (1988). Homology in classical and molecular biology. *Molecular Biology and Evolution*, *5*, 603–625. https://doi.org/10.1093/oxfordjournals.molbev.a040523

Sandeman, D. C., Scholtz, G., & Sandeman, R. E. (1993). Brain evolution in decapod Crustacea. *Journal of Experimental Zoology*, *265*, 112–133. https://doi.org/10.1002/jez.1402650204

Sayre, M. E., & Strausfeld, N. J. (2019). Mushroom bodies in crustaceans: Insect-like organization in the caridean shrimp *Lebbeus groenlandicus*. *Journal of Comparative Neurology*, *527*, 2371–2387.

Skoulakis, E. M., Kalderon, D., & Davis, R. L. (1993). Preferential expression in mushroom bodies of the catalytic subunit of protein kinase A and its role in learning and memory. *Neuron*, *11*, 197–208.

Strausfeld, N. J. (2020). *Nomen est omen*, cognitive dissonance, and homology of memory centers in crustaceans and insects. *Journal of Comparative Neurology*, *528*, 2595–2601. https://doi.org/10.1002/cne.24919

Strausfeld, N. J., & Sayre, M. E. (2020). Mushroom bodies in Reptantia reflect a major transition in crustacean brain evolution. *Journal of Comparative Neurology*, *528*, 261–282. https://doi.org/10.1002/cne.24752

Strausfeld, N. J., & Sayre, M. E. (2021). Shore crabs reveal novel evolutionary attributes of the mushroom body. *eLife*, *10*, e65167. https://doi.org/10.7554/eLife.65167

Strausfeld, N. J., Wolff, G. H., & Sayre, M. E. (2020). Mushroom body evolution demonstrates homology and divergence across Pancrustacea. *eLife*, *9*, e52411. https://doi.org/10.7554/eLife.52411

Sztarker, J., & Tomsic, D. (2008). Neuronal correlates of the visually elicited escape response of the crab Chasmagnathus upon seasonal variations, stimuli changes and perceptual alterations. *Journal of Comparative Physiology A*, *194*, 587–596. https://doi.org/10.1007/s00359-008-0333-3123

Thoen, H. H., Marshall, J., Wolff, G. H., & Strausfeld, N. J. (2017). Insect-like organization of the stomatopod central complex: Functional and phylogenetic implications. *Frontiers in Behavioral Neuroscience*, *11*, 12.

Thoen, H. H., Wolff, G. H., Marshall, J., Sayre, M. E., & Strausfeld, N. J. (2020). The reniform body: An integrative lateral protocerebral neuropil complex of Eumalacostraca identified in Stomatopoda and Brachyura. *Journal of Comparative Neurology*, *528*, 1079–1094. https://doi.org/10.1002/cne.24788

Tomsic, D., Massoni, V., & Maldonado, H. (1993). Habituation to a danger stimulus in two semiterrestrial crabs: Ontogenic, ecological and opioid modulation correlates. *Journal of Comparative Physiology A*, *173*, 621–633. https://doi.org/10.1007/BF00197770

Tomsic, D., & Romano, A. (2013). A multidisciplinary approach to learning and memory in the crab *Neohelice* (*Chasmagnathus*) *granulata*. In R. Menzel & P. R. Benjamin (Eds.), *Handbook of behavioral neuroscience* (Vol. 22, pp. 337–355). Elsevier. https://doi.org/10.1016/B978-0-12-415823-8.00026-5

Wolfe, J. M., Breinholt, J. W., Crandall, K. A., Lemmon, A. R., Lemmon, E. M., Timm, L. E., Siddall, M. E., & Bracken-Grissom, H. D. (2019). A phylogenomic framework, evolutionary timeline and genomic resources for comparative studies of decapod crustaceans. *Proceedings of the Royal Society B: Biological Sciences*, *286*, 20190079. https://doi.org/10.1098/rspb.2019.0079

Wolff, G., Harzsch, S., Hansson, B. S., Brown, S., & Strausfeld, N. (2012). Neuronal organization of the hemiellipsoid body of the land hermit crab, *Coenobita clypeatus*: Correspondence with the mushroom body ground pattern. *Journal of Comparative Neurology*, *520*, 2824–2846. https://doi.org/10.1002/cne.23059

Wolff, G., Thoen, H. H., Marshall, N. J., Sayre, M. E., & Strausfeld, N. J. (2017). An insect-like mushroom body in a crustacean brain. *eLife*, *6*, e29889. https://doi.org/10.7554/eLife.29889

Wolff, G. H., & Strausfeld, N. J. (2015). Genealogical correspondence of mushroom bodies across invertebrate phyla. *Current Biology*, *25*, 38–44. https://doi.org/10.1016/j.cub.2014.10.049

How to cite this article: Strausfeld NJ. Mushroom bodies and reniform bodies coexisting in crabs cannot both be homologs of the insect mushroom body. *J Comp Neurol*. 2021;529:3265–3271. https://doi.org/10.1002/cne.25152