

Morphological diversification of defensive glands in Corydoradinae catfishes indicates a mixed Müllerian–Batesian mimicry system

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Axillary and pectoral-fin spine glands play a central role in the defensive biology of Siluriformes by releasing toxic secretions; however, their distribution, structural diversity, and evolutionary significance within Corydoradinae remain poorly understood. Here, we present the first comparative histological analysis of these glands across seven genera of Corydoradinae. Axillary glands were present in all examined genera and exhibited a conserved lobular organization consistent with a holocrine secretion type as described previously in other Siluriformes. In contrast, venom-associated pectoral spine glands were restricted to a clade comprising *Hoplisoma*, *Brochis*, and *Osteogaster*. In these genera, gland position and cellular morphology closely match venom glands described in other siluriform lineages, supporting a lineage-specific derived condition. Conversely, *Corydoras*, *Aspidoras*, *Scleromystax*, and *Gastrodermus* lacked true venom-associated pectoral spine glands and instead displayed abundant epidermal granular cells and club cells, consistent with the retention of a non-venomous ancestral state. This pattern is congruent with phylogenetic relationships and implies that mimicry rings may involve Müllerian, quasi-Batesian, and Batesian components depending on their species composition and the degree of defense exhibited by the species present.

Keywords: Aposematism, Axillary gland, Callichthyidae, Pectoral-fin spine gland, Siluriformes.

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Las glándulas axilares y de las espinas pectorales desempeñan un papel central en la biología defensiva de los Siluriformes al liberar secreciones tóxicas; sin embargo, su distribución, diversidad estructural y significado evolutivo dentro de Corydoradinae siguen siendo poco comprendidos. Aquí presentamos el primer análisis histológico comparativo de estas glándulas en siete géneros de Corydoradinae. Las glándulas axilares estuvieron presentes en todos los géneros examinados y exhibieron una organización lobular conservada, consistente con una secreción holocrina descrita previamente en otros Siluriformes. En contraste, las glándulas venenosas asociadas a las espinas pectorales estuvieron restringidas a un clado que comprende *Hoplisoma*, *Brochis* y *Osteogaster*. En estos géneros, la posición glandular y la morfología celular coinciden con las glándulas de veneno descritas en otros linajes de Siluriformes, respaldando una condición derivada específica de este linaje. Por el contrario, *Corydoras*, *Aspidoras*, *Scleromystax* y *Gastrodermus* carecen de verdaderas glándulas venenosas asociadas a las espinas pectorales y presentan abundantes células granulares epidérmicas y células club, consistentes con la retención de un estado ancestral no venenoso. Este patrón es congruente con las relaciones filogenéticas e implica que los anillos de mimetismo pueden involucrar componentes Müllерianos, quasi-Batesianos y Batesianos según su composición y el grado de defensa de las especies presentes.

Palabras clave: Aposematismo, Callichthyidae, Glándula axilar, Glándula de la espina pectoral, Siluriformes.

INTRODUCTION

Many animal species produce toxic chemical substances used for defense against predators, parasites and pathogens. These substances are referred to as toxins, and when they are associated with specialized morphological structures that facilitate their delivery, they are classified as venoms (*e.g.*, the fangs of vipers or the spines of stonefish) (Nelsen *et al.*, 2014; Hildebrandt *et al.*, 2023). Research on animal venoms has historically focused on terrestrial taxa, particularly arthropods, amphibians, reptiles, and a few mammalian lineages, while aquatic organisms have received comparatively less attention (Casewell *et al.*, 2012; Smith *et al.*, 2016). This bias largely reflects logistical difficulties in sampling and preserving venomous tissues in aquatic environments, as well as the perception that these animals pose relatively low risk to humans (Ziegman, Alewood, 2015; Ndandala *et al.*, 2023).

Nevertheless, recent phylogenetic and morphological studies suggest that fishes may represent the vertebrate group with the largest number of venomous species, with estimates ranging from 2,386 to 2,962 species worldwide (Smith, Wheeler, 2006; Smith *et al.*, 2016). Venom systems in fishes are thought to have evolved independently between 18 to 20 times and occur across 50 and 63 different families. These include representatives of Chondrichthyes (*e.g.*, chimaeras, stingrays, horn sharks, and dogfish), Anguilliformes (*e.g.*, *Monognathus* Bertin, 1937), Siluriformes (catfishes), Batrachoididae, Acanthuriformes (scats, rabbitfishes, and surgeonfishes), Scorpaeniformes (weeverfishes,

gurnard perches, stonefishes, and scorpionfishes), Uranoscopidae, *Acyrtus* Schultz, 1944, *Meiacanthus* Norman, 1944, and Carangidae (Smith *et al.*, 2016). In most fish lineages, venom is delivered through dorsal or pectoral fin spines associated with venom glands and functions primarily as an antipredator defense. In contrast, a few taxa employ venomous fangs for predation, as documented in *Meiacanthus* (Halstead, 1988; Smith, Wheeler, 2006; Smith *et al.*, 2016; Harris, Jenner, 2019).

Among fishes, catfish constitute the most species-rich clade of venomous taxa, with estimates ranging from 1,250 to 1,625 species, primarily inhabiting freshwater ecosystems (Wright, 2009; Smith *et al.*, 2016). Their venom apparatus typically consists of a lockable, sharp, and ossified pectoral-fin spine flanked or covered by the spine gland and enclosed within a tegumentary sheath of dermal or epidermal origin. The spine gland is usually located distally along the spine and lacks associated ducts or musculature (Perrière, Goudey-Perrière, 2003; Wright, 2009). The evolutionary origin of this apparatus remains debated. Some authors propose between one and three independent origins within Siluriformes: one in Silurioidei, a second in Callichthyidae (subfamily Corydoradinae), and a third in Doradidae, based on distinctive morphological traits (Wright, 2009, 2015). Other studies have proposed a single early origin of venom systems in Siluriformes, followed by multiple secondary losses or morphological modifications of the spine gland along the phylogeny (Smith *et al.*, 2016). However, the latter hypothesis is based on limited taxon sampling that excludes non-venomous genera within Callichthyidae, among others. When a more comprehensive sampling of Siluriformes is considered (Wright, 2009), scenarios involving two or three independent origins with subsequent reversals appear more likely.

In addition to pectoral spine-associated venom glands, several studies have documented the presence of axillary glands in catfishes. These glands are independent epidermal secretory structures with potential toxic or deterrent functions and have been reported across multiple families of Siluriformes. Axillary glands are typically located beneath the axillary pore near the base of the pectoral spine and are encapsulated by connective tissue (Reed, 1907; Halstead *et al.*, 1953; Cameron, Endean, 1971; Whitear *et al.*, 1991; Carvalho *et al.*, 2021; Sodré *et al.*, 2021). Their secretion is frequently described as milky and protein-rich, released under stress conditions and sometimes accompanied by acoustic signals produced by spine movement or swim bladder vibration (Greven *et al.*, 2006; Sodré *et al.*, 2021). Although axillary secretions have been hypothesized to act synergistically with the spine venom apparatus, their high solubility and distinct histological organization suggest that they might instead function as complementary defensive tissues, releasing alarm or deterrent substances into the surrounding water (Whitear *et al.*, 1991; Wright, 2012).

Among the groups possessing venom apparatuses, the Corydoradinae represents one of the most diverse and distinctive lineages of Neotropical catfishes, comprising approximately 208 species distributed from the eastern slopes of the Andes to the Atlantic coast and the Río de la Plata basin (Britto, 2003; Alexandrou *et al.*, 2011; Dias *et al.*, 2024). Corydoradinae currently includes seven monophyletic genera (Dias *et al.*, 2024), with *Corydoras* Lacepède, 1803 as the sister clade to all remaining taxa: *Aspidoras* Ihering, 1907, *Scleromystax* Günther, 1864, *Gastrodermus* Cope, 1878, *Osteogaster* Cope, 1894, *Brochis* Cope, 1871, and *Hoplisoma* Swainson, 1838 (Dias *et al.*, 2024; Alonso *et al.*, 2025). These species are well known among aquarists and local communities for their

conspicuous coloration patterns and the painful stings inflicted by their pectoral spines, which have been associated with the capacity of axillary glands to secrete presumably toxic substances under stress (Greven *et al.*, 2006; Kiehl *et al.*, 2006).

Consistent with these traits, several studies have documented Müllerian mimicry rings within Corydoradinae, assuming all lineages produce venom and can defend themselves against predators. Alexandrou *et al.* (2011) described 24 Müllerian mimicry rings involving at least 52 species, with 92% of them formed by two to three different evolutionary lineages. They showed that lineages with divergent snout morphologies, reflecting ecological differentiation in feeding strategies, often coexist while sharing similar aposematic coloration patterns likely associated with chemical defenses. In addition, Lima, Sazima (2017) provided the first evidence for a potential Batesian mimicry system within this complex. They suggested that species of the genus *Corydoras* (Lineage 1 in Alexandrou *et al.*, 2011), which possess serrated but comparatively less pungent pectoral spines, may function as Batesian mimics of *Hoplisoma* species (Lineages 6 and 9), which have more pungent spines and are relatively more abundant than *Corydoras* when they co-occur.

Together, these studies highlight Corydoradinae as an interesting model system for investigating the presence of both Batesian and Müllerian mimicry in this group. However, a critical gap remains in the distinction between axillary glands and pectoral spine glands, particularly regarding which structures are responsible for venom production and whether both gland types are present across all genera. Herein, we aim to characterize the histological and morphological structure of axillary and pectoral spines glands in Corydoradinae, compare their presence among genera, and assess their implications for defensive strategies and mimicry patterns.

MATERIAL AND METHODS

Specimen acquisition. A total of 51 specimens representing all recognized genera of Corydoradinae were examined. Specimens were obtained from multiple sources, including the aquarium trade, field collections, and ichthyological collections housed at the Universidade Federal do Rio Grande do Sul, Porto Alegre (UFRGS) and the Instituto de Ciencias Naturales (ICN) of the Universidad Nacional de Colombia, Bogotá. Detailed information for each specimen, including voucher catalog numbers, provenance, and taxonomic identification, is provided in Tab. S1.

Gross anatomy and dissections. Specimens obtained from field collections and the aquarium trade were euthanized using MS-222 or eugenol, fixed in 10% formalin, and subsequently transferred to 70% ethanol for preservation. Specimens from ichthyological collections had been previously fixed in 10% formalin and preserved in 70% ethanol. For each specimen, sex was determined, and standard length (SL) was measured. External morphological features, including the presence of an axillary pore and, when discernible, the external visualization of the axillary gland, were recorded. The pectoral spine and associated axillary gland were dissected from each specimen (Fig. 1). In cases where the axillary gland was not macroscopically evident, tissue underlying the cleithrum was dissected to ensure the inclusion of the axillary region within this tissue. All dissected tissues were stored in 70% ethanol until histological processing.

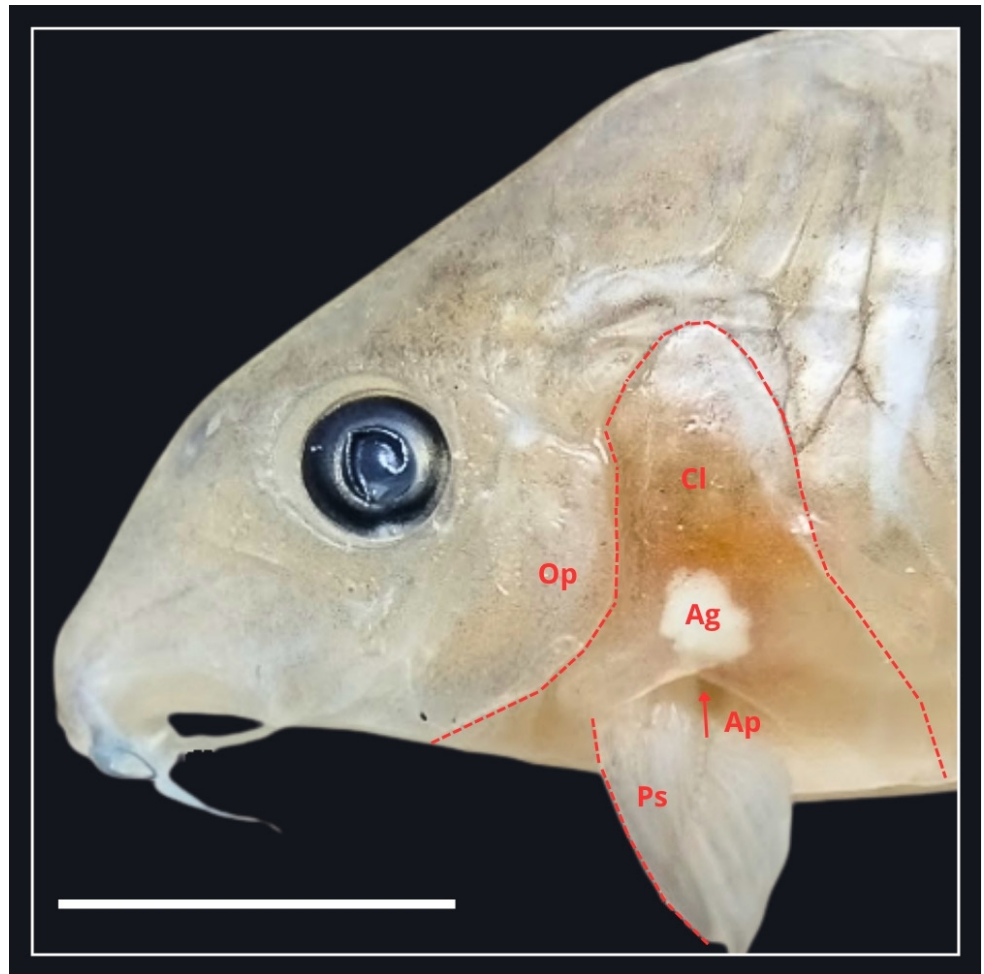


FIGURE 1 | External anatomy of the anterior lateral region of *Brochis* sp. (non-catalogued). Incision used to expose the axillary gland and the position of the pectoral spine (red dotted line), opening of the axillary pore (red arrow), operculum (Op), cleithrum (Cl), axillary gland (Ag), axillary pore (Ap), pectoral spine (Ps). White scale bar represents 1 cm.

Histological procedures. Dissected pectoral spines and axillary gland tissues were processed using standard histological protocols. Samples were decalcified in 10% nitric acid, dehydrated in increasing concentrations of alcohols, cleared in xylene, impregnated, and embedded in paraffin. Paraffin blocks were sectioned on a rotary microtome to obtain histological sections 3–5 μm in thickness. Sections were mounted on glass slides, rehydrated through a descending ethanol series, and stained with hematoxylin and eosin (H&E) following conventional protocols (Ross, Pawlina, 2018). Specimens from UFRGS were embedded in resin and stained with toluidine blue due to availability and to enhance tissue contrast and cellular details. Selected samples were also stained with periodic acid–Schiff (PAS) and Masson’s trichrome to evaluate the presence of mucopolysaccharides and to further characterize histochemical and connective tissue features. All sections were examined and photographed using light microscopy (Leica© DM500).

RESULTS

All seven genera (*Corydoras*, *Aspidoras*, *Scleromystax*, *Gastrodermus*, *Osteogaster*, *Brochis*, and *Hoplisoma*) possessed an axillary gland located beneath the cleithrum in the axillary region and associated with an external axillary pore near the base of the pectoral fin. In contrast, the presence and morphology of pectoral spine glands varied among genera, displaying clear histological and structural differences.

Axillary gland. Axillary glands were present in all examined genera as paired (one at each side), whitish, encapsulated structures with an irregular to rounded shape, measuring approximately 0.5–2 mm in diameter. These glands were consistently located adjacent to an axillary pore at the base of the pectoral fin (Fig. 2). Histologically, each gland was enclosed by a connective tissue capsule of variable thickness and bordered by adjacent muscle fibers, adipose tissue, and skeletal elements. Internally, the gland exhibited a lobular organization, with distinct lobules containing abundant granular secretory material in most specimens (Fig. 3).

Secretory cells measured approximately 20 to 60 μm in diameter and were characterized by large nuclei and a granular cytoplasm. In several sections, cells were observed disintegrating and releasing dense cytoplasmic granules into the glandular lobules, consistent with a holocrine mode of secretion (Fig. 4). Lobules were separated by connective septa containing small to elongated nuclei and occasional blood vessels with visible erythrocytes.

In several specimens of *Hoplisoma* (*H. armatus* (Günther, 1868), *H. axelrodi* (Rössel, 1962), *H. leucomelas* (Eigenmann & Allen, 1942), *H. loxozonum* (Nijssen & Isbrücker, 1983), *H. metae* (Eigenmann, 1914), and *H. reynoldsi* (Myers & Weitzman, 1960)), as well as *Brochis* (*B. arcuata* (Elwin, 1938) and *B. delphax* (Nijssen & Isbrücker, 1983)), the glandular secretion appeared predominantly colloid-like, forming homogeneous or partially fused masses. In these regions, secretory cells with a uniform, pale cytoplasm, and binucleated cells were frequently observed. In specimens from different genera, both secretion types co-occurred, with regions containing colloid-like material adjacent to lobules with granular secretions (Fig. 4C).

Pectoral-fin spine glands. Pectoral spine glands exhibited marked intergeneric variation in their presence, structure, and histological organization across Corydoradinae. Two main patterns were observed: (1) the presence of a well-developed glandular tissue associated with the pectoral spine, and (2) the absence of such tissue, with the spine instead covered by epidermal layers of variable thickness and cellular composition.

A conspicuous glandular tissue was identified exclusively in the clade comprising *Osteogaster*, *Brochis*, and *Hoplisoma*. This tissue consisted of a compact layer of round to polygonal secretory cells (20–50 μm in diameter) with uniform eosinophilic cytoplasm and centrally positioned nuclei. The glandular layer was located adjacent to the bony pectoral spine in its distal region and was externally covered by an epidermal layer (Figs. 5A–D). Based on its morphology and position, this structure is herein identified as the venom gland.

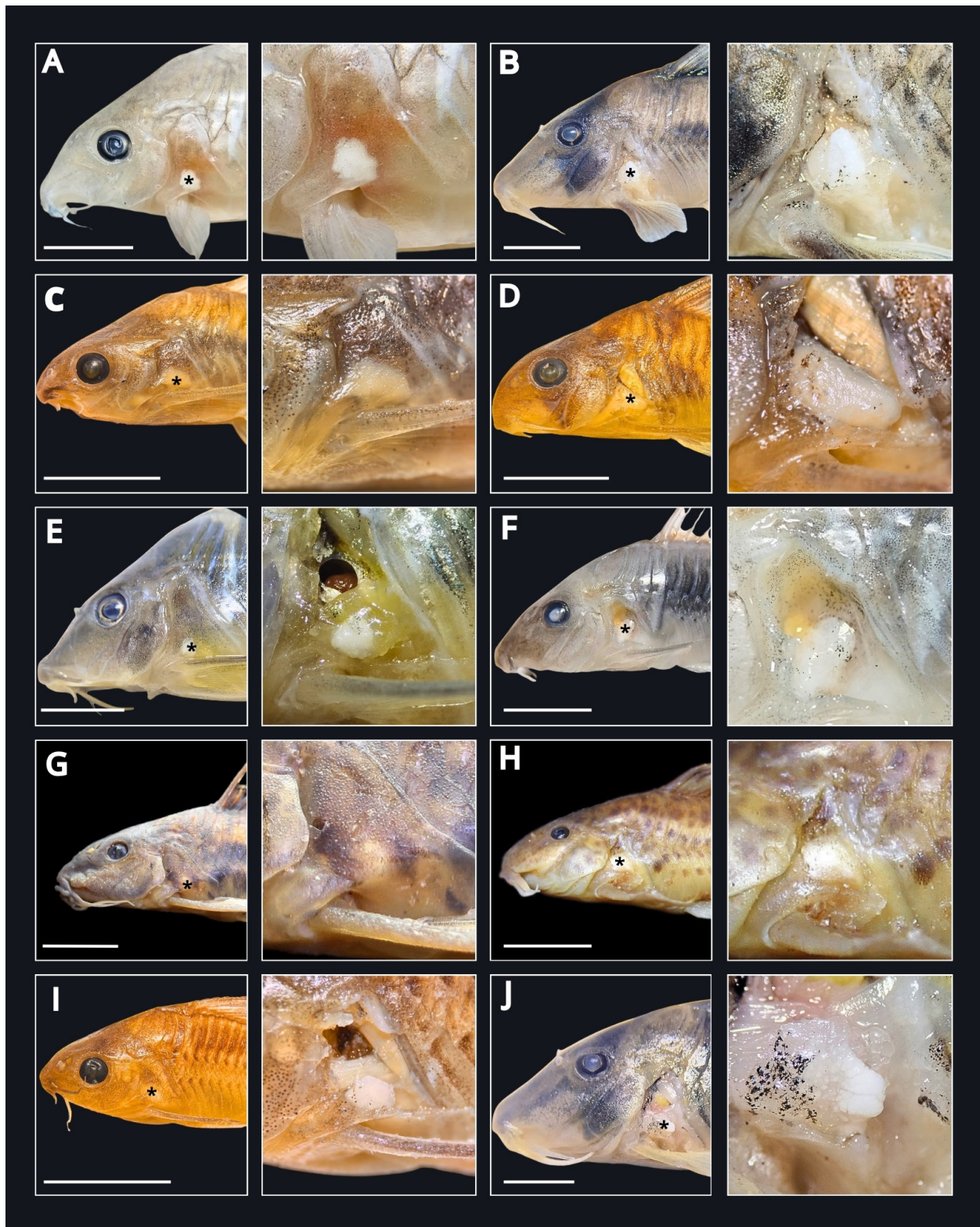


FIGURE 2 | Axillary glands in seven genera of Corydoradinae. Left column showing the position in relation to the head, with the axillary gland marked with an asterisk. Right column in a zoom showing the structure. **A.** *Brochis* sp. (non-catalogued); **B.** *Corydoras simulatus* (ICN 25509); **C.** *Gastrodermus pygmeus* (ICN 14814); **D.** *Hoplisoma reynoldsi* (ICN 29071); **E.** *Brochis splendens* (ICN 26511); **F.** *Osteogaster aeneus* (ICN 26507); **G.** *Scleromystax macropterus* (UFRGS 29647); **H.** *Aspidoras fuscoguttatus* (UFRGS 10522); **I.** *Gastrodermus elegans* (ICN 14252); **J.** *Corydoras septentrionalis* (ICN 26509). White scale bar represents 1 cm.

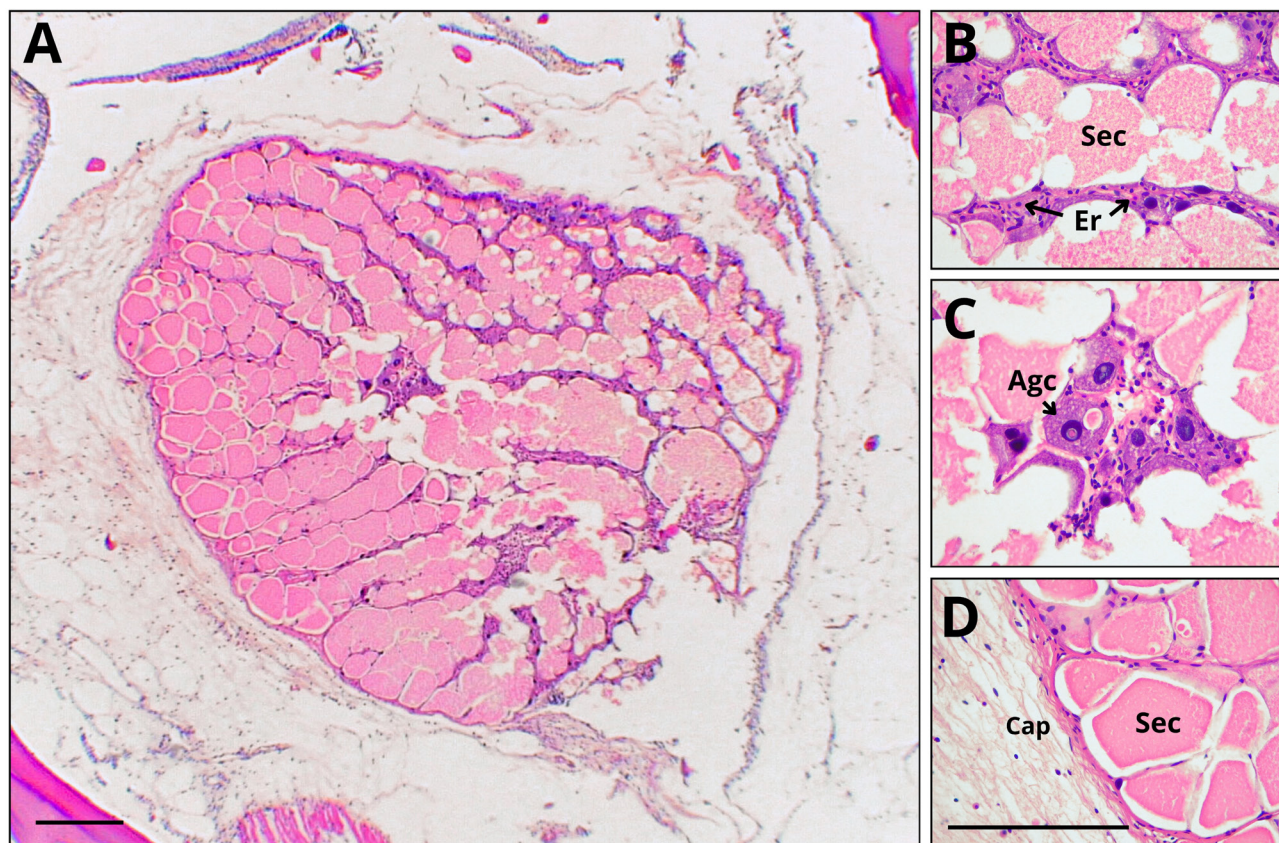


FIGURE 3 | Longitudinal section of the axillary gland of *Brochis splendens* (ICN 26511). **A.** General view of the gland and surrounding tissues. **B.** Connective tissue septa dividing the adjacent glandular lobules. **C.** Secretory cells of the axillary gland. **D.** Capsule and adjacent lobule of the axillary gland. Secretion (Sec), erythrocytes (Er), axillary gland cells (Agc), capsule (Cap). Black scale bar represents 100 µm.

In *B. splendens* (Castelnau, 1855) (Fig. 5A), the glandular layer reached approximately 200 µm in thickness. The overlying epidermis contained keratinocytes, goblet cells, and club cells, the latter recognizable by their clearer cytoplasm. In *H. metae* and *O. melanotaenia* (Regan, 1912) (Figs. 5B, D), the epidermis additionally included granular secretory cells similar to those observed in *Corydoras* and in the axillary gland, although these cells were less abundant and less developed. In some species, such as *H. loxozonum* and certain individuals of *B. delphax*, the epidermis did not completely cover the underlying glandular tissue.

Hoplisoma araguaiaense (Sands, 1990) displayed a distinctive pectoral spine morphology relative to other species of the genus. In this species, the spine was predominantly covered by an epidermis rich in club cells, along with an additional cell type lacking a visible nucleus and exhibiting a darker, occasionally granular cytoplasm.

No comparable glandular tissue was observed along the entire length of the pectoral spine in *Corydoras*, *Aspidoras*, *Scleromystax*, or *Gastrodermus*. In these genera, the spine was covered by an epidermis of variable thickness composed primarily of keratinocytes, goblet cells, and club cells, and occasionally containing eosinophilic granular secretory cells (Figs. 5E–H).

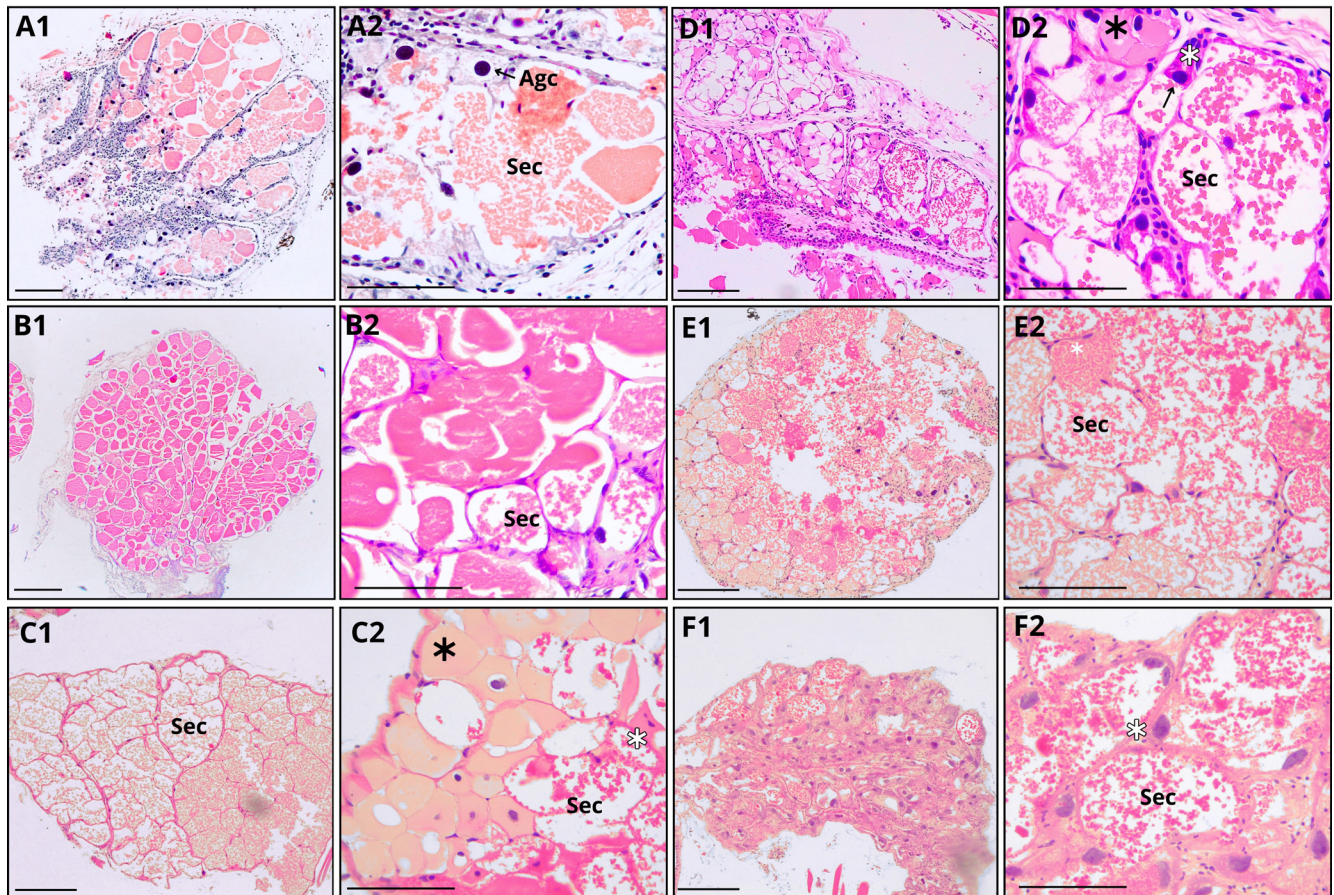


FIGURE 4 | Variation in the axillary gland architecture among Corydoradinae specimens. **A.** Axillary gland of *Brochis delphax* (ICN 26512), showing a lobular organization with granular secretion; Basophilic glandular cells release eosinophilic material. **B.** Axillary gland of *Corydoras simulatus* (ICN 25509) with uniformly granular secretion. **C.** Axillary gland of *Hoplisoma reynoldsi* (ICN 29071), characterized by glandular cells with a uniform appearance and pale pink cytoplasm in the periphery of the gland. **D.** Axillary gland of *Hoplisoma metae* (ICN 26508), displaying the coexistence of both secretory cell types. **E.** Axillary gland of *Gastrodermus elegans* (ICN 14252). **F.** Axillary gland of *Corydoras pastazensis* (ICN 10311). For each specimen, panels 1 and 2 represent magnifications of 100× and 400×, respectively. Uniform glandular cells (black asterisks), granular glandular cells (white asterisks), axillary glandular cells (Agc), secretion (Sec). Black scale represents 100 µm.

Within the clade comprising *Aspidoras* (*A. albatro* Nijssen & Isbrücker, 1976) and *Scleromystax* (*S. macropterus* (Regan, 1913), *S. virgulatus* (Nijssen & Isbrücker, 1980)), the relatively thin pectoral spine was covered by an epidermis containing multiple layers of club cells measuring approximately 30–50 µm in diameter. These cells exhibited pale, homogeneous cytoplasm and centrally located nuclei and were present both along the spine and in its basal region (Figs. 5G–H). Club cells were more abundant in *Aspidoras* than in *Scleromystax*, although large aggregates were occasionally observed in the latter. In *Gastrodermus elegans*, the epidermis covering the pectoral spine was poorly developed and consisted predominantly of keratinocytes, with no evidence of specialized secretory cell types.

In *Corydoras* (*C. pastazensis* Weitzman, 1963, *C. semiaquilus* Weitzman, 1964, and *C. simulatus* Weitzman & Nijssen, 1970), the pectoral spine exhibited large serrations

covered by a well-developed, highly secretory epidermis. This epidermis contained abundant eosinophilic granular secretory cells (20–50 μm in diameter) resembling those described for the axillary gland (Figs. 5E–F). The secretory epidermis extended along the entire length of the spine and included keratinocytes, blood vessels containing erythrocytes, and occasional club and goblet cells.

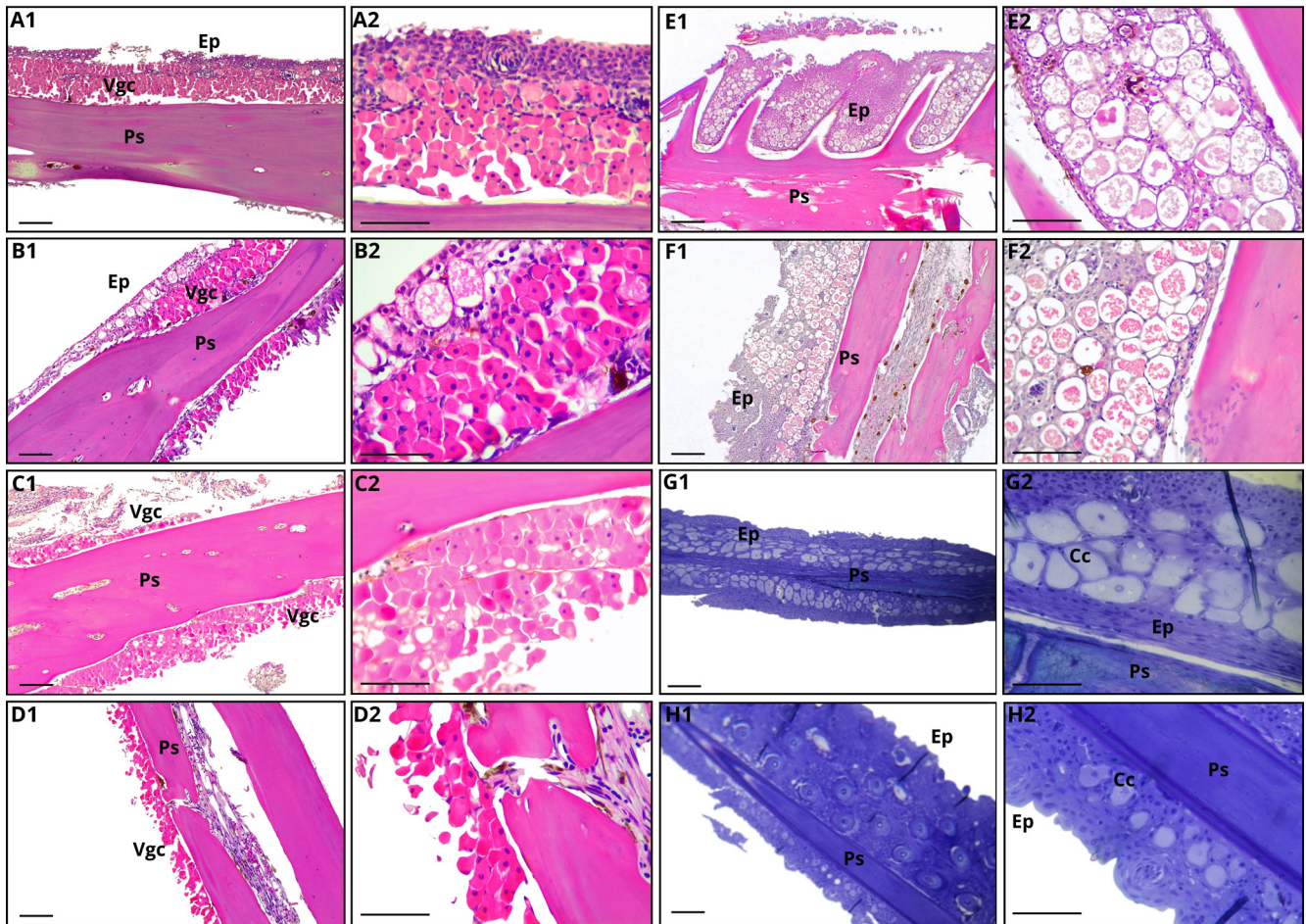


FIGURE 5 | Longitudinal histological sections of the pectoral spine showing differences between venom-bearing and non-venom-bearing genera of Corydoradinae. **A.** *Brochis splendens* (ICN 26511), showing the venom gland adjacent to the pectoral spine and covered by an epidermal layer. **B.** *Hoplisoma metae* (ICN 25479), with an epidermis containing granular secretory cells overlying the venom gland. **C.** *Hoplisoma leucomelas* (ICN 15840). **D.** *Osteogaster melanotaenia*. **E.** *Corydoras simulatus* (ICN 25509), in which no previously described venom gland is present; instead, a highly developed epidermis with abundant eosinophilic granular secretory cells occurs between the spine serrations. **F.** *Corydoras semiaquilus* (ICN 16865). **G.** *Aspidoras albater* (UFRGS 9906) displays a thin spine covered by a layer of club cells and keratinocytes. Stained with toluidine blue. **H.** *Scleromystax virgulatus* (UFRGS 11026). Stained with toluidine blue. For each specimen, panels 1 and 2 represent magnifications of 100 $\times$ and 400 $\times$, respectively. Venom gland cells (Vgc), epidermis (Ep), pectoral spine (Ps), Club cells (Cc). Black scale bar represents 100 μm .

DISCUSSION

Axillary gland. The axillary gland has been reported in several families of Siluriformes (Reed, 1907; Halstead *et al.*, 1953; Whitear *et al.*, 1991; Greven *et al.*, 2006; Carvalho *et al.*, 2021; Sodré *et al.*, 2021; Egge, 2025), as well as in the toadfish family Batrachoididae (Reed, 1924; Maina *et al.*, 1998; Wright, 2012). It is commonly described as a subcutaneous structure located beneath the posthumeral process of the cleithrum and typically associated with an axillary pore at the base of the pectoral spine. This pore is thought to serve as the external outlet for a multifunctional secretion released to the surrounding environment (Reed, 1907; Halstead *et al.*, 1953; Birkhead, 1972; Whitear *et al.*, 1991; Greven *et al.*, 2006; Carvalho *et al.*, 2021; Sodré *et al.*, 2021). In some taxa, such as *Hassar orestis* (Steindachner, 1875), multiple pores are distributed throughout the axillary region, with each pore corresponding to a small individual gland (Reed, 1924). By contrast, in large-bodied catfishes such as *Ictalurus punctatus* (Rafinesque, 1818), axillary pores close early in ontogeny (Birkhead, 1972), whereas in heavily armored or naked species with reduced or loosely articulated spines, the pore is absent altogether (Reed, 1924). In Corydoradinae, the axillary gland is present in all examined genera and conforms to the described Siluriformes condition, being positioned beneath the cleithrum and associated with a single axillary pore.

Histologically, the axillary gland in Siluriformes has been described as sacciform (Wright, 2012) or pyriform (Reed, 1907; Halstead *et al.*, 1953; Cameron, Endean, 1971; Carvalho *et al.*, 2021), with reported sizes ranging from approximately 2.0 mm in *Ariopsis felis* (Linnaeus, 1766) (Halstead *et al.*, 1953) to 5 mm in *Noturus flavus* Rafinesque, 1818 and up to 20 mm in *Cnidogobius macrocephalus* (Valenciennes, 1840) (Reed, 1907; Cameron, Endean, 1971). In Corydoradinae, axillary glands were predominantly round to oval, ranging from approximately 0.5 mm in smaller species to 2 mm in the largest examined specimen. These dimensions are consistent with those reported for similarly sized Siluriformes, such as *Brachyramphidia* spp. (Carvalho *et al.*, 2021). As in other catfishes, the glands were enclosed by a connective tissue capsule and often surrounded by adipose tissue. Connective tissue septa extended inward from the capsule, subdividing the gland into lobules or saccular units. Although a tubular organization has been previously described for one individual of *Osteogaster aeneus* (Gill, 1858) (Greven *et al.*, 2006), our histological observations based on 51 individuals of Corydoradinae indicate a lobular architecture separated by connective septa (Fig. 3).

The cellular composition of the axillary gland consists primarily of secretory cells supported by a network of non-secretory cells. Secretory cells are the main constituent of the gland and are responsible for producing the glandular secretion. In Siluriformes, these cells are typically large and polygonal, ranging from 75 to 100 µm in diameter (Reed, 1924; Wright, 2012; Carvalho *et al.*, 2021) and reaching up to 210 µm in *A. felis* (Halstead *et al.*, 1953). They are characterized by large nuclei and a vacuolated cytoplasm that undergoes a progressive transformation from basophilic and frequently binucleated in immature stages to eosinophilic and anucleated in mature stages (Halstead *et al.*, 1953; Cameron, Endean, 1971; Carvalho *et al.*, 2021; Sodré *et al.*, 2021; Egge, 2025). A similar gradient of cellular differentiation was observed in Corydoradinae. Immature cells display pale, occasionally binucleated cytoplasm, whereas more advanced stages were characterized by cells with granular cytoplasm and large nuclei that eventually

disintegrated, releasing eosinophilic material into the glandular lobules. Different stages of cellular maturation were frequently observed within the same lobule, suggesting a continuous cycle of secretory cell differentiation and degeneration (Fig. 4).

Supporting cells were primarily located within the connective tissue septa, displaying elongated (filiform) nuclei and indistinct cytoplasm, forming a delicate scaffold surrounding the secretory cells (Cameron, Endean, 1971). In Corydoradinae, these septa were sparsely vascularized, in contrast to the highly vascularized condition reported for *Acanthodoras spinosissimus* (Eigenmann & Eigenmann, 1888) (Sodré *et al.*, 2021), although some capillaries were occasionally observed. In addition, muscle fibers, adipose tissue, and immune cells were present around the axillary gland, consistent with previous descriptions in other siluriform species (Reed, 1907; Halstead *et al.*, 1953; Cameron, Endean, 1971; Carvalho *et al.*, 2021).

The glandular lumen of the axillary gland in Siluriformes has been described as extremely narrow or even absent, with no evidence of a well-defined duct for secretion transport. This condition suggests a holocrine mode of secretion, in which the secretory products are released when the secretory cells disintegrate (Cameron, Endean, 1971; Whitear *et al.*, 1991; Carvalho *et al.*, 2021). An exception has been reported for *O. aeneus*, in which a distinct lumen enabling glandular discharge was described (Greven *et al.*, 2006). Our observations support the absence of a distinct lumen or duct in the axillary glands of Corydoradinae, further supporting a holocrine mechanism whereby secretory cells within each lobule disintegrate, releasing their contents and progressively filling the lobular cavity. The accumulated material was predominantly eosinophilic and occasionally formed reddish vesicles or a pink, granular secretion (Fig. 4). Under stress conditions, the secretion appeared transparent and contained minute white droplets, differing from the whitish, milky secretion reported for *A. spinosissimus* (Sodré *et al.*, 2021). Personal observations under stress-induced conditions documented secretions with similar features in Corydoradinae species; nevertheless, future studies should expand protein quantification and identification analyses to elucidate the true nature of its function.

Axillary glands are present in all examined genera of Corydoradinae. However, we were unable to find evidence in the literature for the presence of axillary glands in Callichthyinae (*Callichthys* Scopoli, 1777, *Dianema* Cope, 1871, *Hoplosternum* Gill, 1858, *Leptoplosternum* Reis, 1997, and *Megalechis* Reis, 1997) (Shimabukuro-Dias *et al.*, 2004), the other subfamily of Callichthyidae. Nonetheless, axillary glands have been reported in multiple Siluriformes families (Egge, 2025), indicating that this structure is widely distributed across the catfish order. Despite its widespread distribution, the functional role of axillary gland secretions remains unresolved and has been the subject of long-standing debate (Egge, 2025). Proposed functions include antimicrobial activity, particularly against a group of aquatic bacteria (*i.e.*, *Vibrio* spp.), which could reduce bacterial growth on the skin surface (Kiehl *et al.*, 2006). Other authors have emphasized a defensive or crinotoxic function, whereby the secretion is released under stress to provoke aversive reactions in potential predators (Al-Hassan *et al.*, 1987; Sodré *et al.*, 2021; Egge, 2025). Additional hypotheses include roles in pheromonal communication, alarm signaling, or ionoregulation (Wright, 2012; Egge, 2025).

Recently, it has been suggested that axillary gland secretions exhibit similar toxicity levels between two species of Corydoradinae (*H. metae* and *C. simulatus*), based on

a toxicity experiment that estimated lethality in shrimps (Phelps *et al.*, 2026). These results indicate that toxicity remains a plausible function of this gland, particularly given that secretion release is commonly associated with stress responses. However, caution is warranted when interpreting these findings, as the natural predators of Corydoradinae are typically larger vertebrates (*e.g.*, birds and larger fishes; Alexandrou *et al.*, 2011), for which toxicity assessed using invertebrate models may not be directly comparable. Further studies focusing on the biochemical and proteomic composition of axillary gland secretions will be essential to elucidate their structural complexity and functional significance.

Pectoral-fin spine glands. In Siluriformes, venom delivery is generally mediated by the dorsal and pectoral spines. These spines possess an ossified core covered by a spine gland and integumentary sheath that releases its contents when the tissue is disrupted during interactions with predators (Halstead *et al.*, 1953; Egge, 2025). The associated venom spine gland has been described as an aggregation of unicellular glandular cells adjacent to the bony spine, and it is thought to be derived from epidermal holocrine cells (Cameron, Endean, 1973). Numerous studies have documented the presence of venom glands associated with the dorsal and pectoral spines across Siluriformes (Reed, 1907, 1924; Halstead *et al.*, 1953; Whitear *et al.*, 1991; Carvalho *et al.*, 2021; Egge, 2025).

This gland is typically described as a subcutaneous structure extending longitudinally along the pectoral spine, becoming progressively more abundant and better developed from the medial toward the distal portions. In *A. felis*, the gland is restricted to the distal two-thirds of the spine and gradually diminishes toward the base (Halstead *et al.*, 1953), a pattern also observed in *Noturus* by Egge, Simons (2010), where the highest glandular density occurs in the distal third of the pectoral spine. Reed (1907) further noted that the gland is often associated with a swelling around the midsection of the spine and may occupy most of the space between the spine and the overlying skin. Similarly, Whitear *et al.* (1991), Bhimachar (1944), and Carvalho *et al.* (2021) reported that the gland lies immediately beneath the epidermis and directly adjacent to the bony spine in *Heteropneustes fossilis* Müller, 1840, and *Brachyrhamdia* spp.

In the Corydoradinae subfamily, in the genera *Hoplisoma*, *Brochis*, and *Osteogaster*, we observed a comparable distribution pattern, with glandular tissue most developed in the middle and distal portions of the pectoral spine and largely absent proximally. As reported for other Siluriformes, the gland in these taxa was situated directly against the bony spine and beneath the epidermal layer. Specific spatial arrangements of glandular tissue have been described in some species, such as *A. felis*, in which glandular cells occur along the anterolateral and posterolateral margins of the spine (Halstead *et al.*, 1953), or along the posterior margin near the posterior serrae, as reported for *Brachyrhamdia* spp. (Carvalho *et al.*, 2021). Wright (2012) documented extensive diversity in glandular arrangements across catfishes. In contrast, we observed glandular tissue along both the anterior and posterior margins of the first pectoral fin ray (the pectoral spine), without evidence of external swellings, longitudinal grooves, or depressions that might indicate the position of the gland, as reported for other taxa (Reed, 1907; Wright, 2012).

Venom gland cells associated with the pectoral spine are typically described as large (12–28 µm in *A. felis*) and formed by polygonal cells arranged in broad sheets or compact aggregates. Their cytoplasm is strongly acidophilic, likely reflecting a high protein

content, and stains more intensely with eosin than surrounding club cells (Halstead *et al.*, 1953; Whitear *et al.*, 1991; Carvalho *et al.*, 2021; Egge, 2025). Reed (1907) initially proposed that venom gland cells arise from the transformation of club cells; however, ultrastructural studies by Whitear *et al.* (1991) demonstrated that these represent distinct cell types. Although Egge, Simons (2010) noted morphological similarities between venom gland cells and club cells in Ictaluridae, they likewise considered them separate entities. In our material, when venom glands were present, club cells were restricted to the epidermis and exhibited a pale cytoplasm, whereas venom gland cells were located beneath the epidermis and displayed a markedly more eosinophilic cytoplasm.

Specifically, Wright (2009) reported contrasting results, documenting the presence of circumferential glandular cells associated with the pectoral spine in *O. aeneus* but absent in *B. splendens*. In contrast, our results support the presence of a shared venom gland morphology within a clade of Corydoradinae, in which the genera *Osteogaster*, *Brochis*, and *Hoplisoma* consistently exhibit this structure.

On the other hand, *Corydoras* exhibits a well-developed epidermis containing abundant keratinocytes, goblet cells, club cells, and conspicuous eosinophilic granular secretory cells, which closely resemble those of the axillary gland (Figs. 5E–F). These eosinophilic granular secretory cells were particularly abundant near the serrations and within the grooves separating the serrae. One possibility is that these cells correspond to the eosinophilic granular cells (EGCs) described by Mokhtar (2022), characterized by an eccentric nucleus and eosinophilic cytoplasmic granules, and generally associated with immune functions. However, EGCs have been mainly reported in the epidermis around the mouth and nasal fossae of fish. Alternatively, these cells may be homologous or functionally related to axillary gland secretory cells, potentially contributing to wound healing, local defense, or chemical signaling in the pectoral fin, an anatomical structure that is highly exposed and frequently prone to mechanical damage.

Gastrodermus exhibited a poorly developed epidermis over the pectoral spine, in some cases appearing completely absent, likely due to its small body size or to preservation artifacts. *Aspidoras* and *Scleromystax* form a clade characterized by similar epidermal morphology, dominated by club cells and keratinocytes, with no evidence of venom glands or eosinophilic granular secretory cells such as those observed in *Corydoras*. Wright (2009) reported the presence of circumferential glandular cells associated with the pectoral spine in *Aspidoras albater*; however, we were unable to confirm this condition in our material, where the epidermis of the spine instead contained numerous club cells (Fig. 5G).

The absence of venom gland morphology in the pectoral spine of *Gastrodermus*, *Aspidoras*, and *Scleromystax* supports the hypothesis that venom-bearing pectoral spine glands represent an evolutionary novelty within a clade of Corydoradinae, comprising *Osteogaster*, *Brochis*, and *Hoplisoma* (Fig. 6). Wright (2009) reported the presence of pectoral spine venom glands in other Callichthyidae, including *Dianema longibarbis* Cope, 1872, *Hoplosternum littorale* (Hancock, 1828), and *Callichthys callichthys* (Linnaeus, 1758), all members of the subfamily Callichthyinae. However, in the only species of this group illustrated by Wright (2009) (*D. longibarbis*, Fig. 2C), the venom gland cells are represented as a tissue composed of multiple round to polygonal cells with clear cytoplasm located within the epidermis. Based on their morphology and epidermal position, these cells more closely resemble epidermal club cells, which also exhibit clear

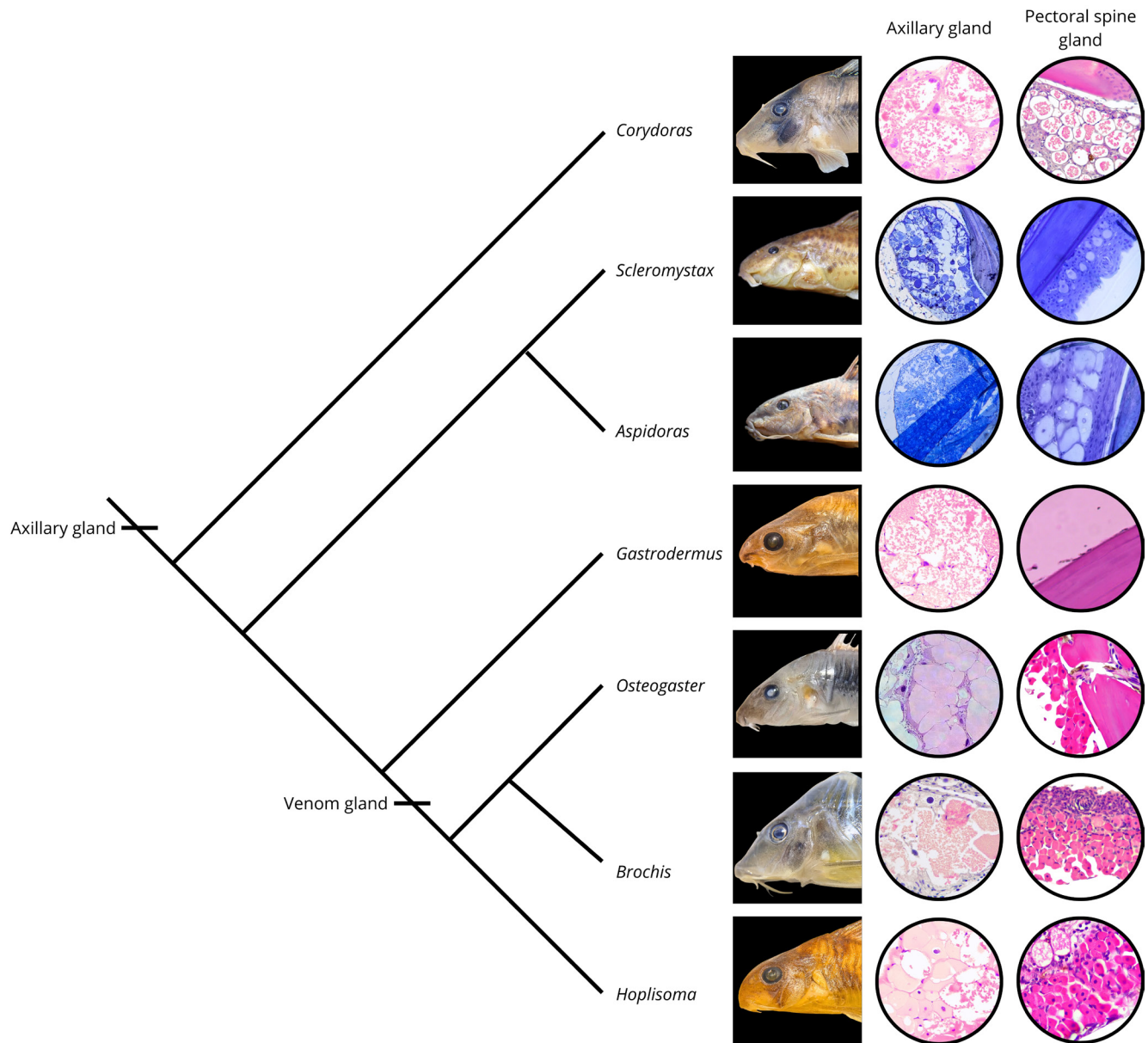


FIGURE 6 | Evolutionary distribution of axillary and pectoral spine glands in Corydoradinae. Simplified phylogeny is based on the molecular hypothesis proposed by Dias *et al.* (2024) and illustrates the presence of axillary glands across all genera of the subfamily, whereas the venom gland associated with the pectoral spine is restricted to a clade comprising *Osteogaster*, *Brochis*, and *Hoplisoma*. Because axillary glands also occur in other families of Siluriformes, their placement in the cladogram is intended for illustrative purposes only and does not represent a synapomorphy of Corydoradinae.

cytoplasm and occur within the epidermis. To accept an alternative interpretation that venom-associated pectoral spine glands evolved multiple times within Callichthyidae, future analyses are needed to check if the glandular tissues reported by Wright (2009) in the pectoral fins of *H. littorale* and *C. callichthys* represent venom gland cells or epidermal club cells.

Implications in mimicry dynamics. Corydoradinae species have long been considered aposematic models due to their combination of an armored integument with a distinctive coloration pattern, the presence of sharp and lockable pectoral and dorsal spines, and the presence of toxic glands (Axenrot, Kullander, 2003; Alexandrou *et al.*, 2011; Lima, Sazima, 2017). Together, these features are likely able to deter predators and constitute an effective evolutionary defense mechanism, making Corydoradinae an ideal system for investigating the ecology and evolutionary dynamics of freshwater mimicry (Ruxton *et al.*, 2018). Importantly, our results indicate that while defensive traits are broadly distributed across the subfamily, they are not equivalent among genera, particularly in the presence of additional venom-associated pectoral spine glands, which may generate differences in defensive effectiveness and influence the type of mimicry involved.

The presence of venom-associated pectoral spine glands only in the clade comprising *Brochis*, *Hoplisoma*, and *Osteogaster* supports a single origin of these glands in the Corydoradinae (Fig. 6). Further, our histological analyses indicate that these glands are absent in *Corydoras*, *Aspidoras*, *Scleromystax*, and *Gastrodermus*. Interestingly, several species from both venom-bearing and non-venom-bearing lineages have been reported to participate in mimicry rings, often forming mixed-species shoals and exhibiting highly convergent color patterns. Alexandrou *et al.* (2011) identified 52 Corydoradinae species forming 24 putative Müllerian mimicry rings, with more than 90% of these rings composed of species from different genera that, nonetheless, share strikingly similar coloration. Classical Müllerian mimicry requires that all participating species are defended, contribute to predator deterrence, and share the costs associated with predator learning a common warning signal (Ruxton *et al.*, 2018). Our results partially support this interpretation, as all examined Corydoradinae possess at least some combination of mechanical and glandular defenses. However, the additional presence of venom-associated pectoral spine glands in only some genera suggests that defensive effectiveness may not be equivalent among lineages.

The armored bodies covered with bony plates and odontodes, together with the ossified spines and their functional locking mechanism, constitute an effective mechanical defense that makes these fishes difficult to swallow, but does not completely prevent predation. For example, individuals of *Corydoras* have been reported among the dietary items of *Hoplias malabaricus* (Bloch, 1794), suggesting that these mechanical defenses can be overcome through predator behavior or by differences in predator-prey size (Loureiro, Hahn, 1996). This indicates that additional defensive mechanisms may further influence predator deterrence and raises important questions regarding the true nature of the proposed mimicry rings. A clear example is mimicry ring 11 described by Alexandrou *et al.* (2011), composed of *C. simulatus* and *H. metae*. Our histological evidence (Fig. 7) demonstrates that *Corydoras* lacks venom-associated pectoral spine glands, whereas *Hoplisoma* possesses them. Because both genera retain armored bodies, locking spines, and axillary glands, both are likely defended to some extent. However, the additional venom-associated pectoral spine glands in *Hoplisoma* suggest asymmetries in defensive effectiveness, indicating that this association may differ from a strictly Müllerian mimicry ring.

Previous studies have already suggested the occurrence of both types of mimicry within Corydoradinae and between Corydoradinae and other Siluriformes (Axenrot,

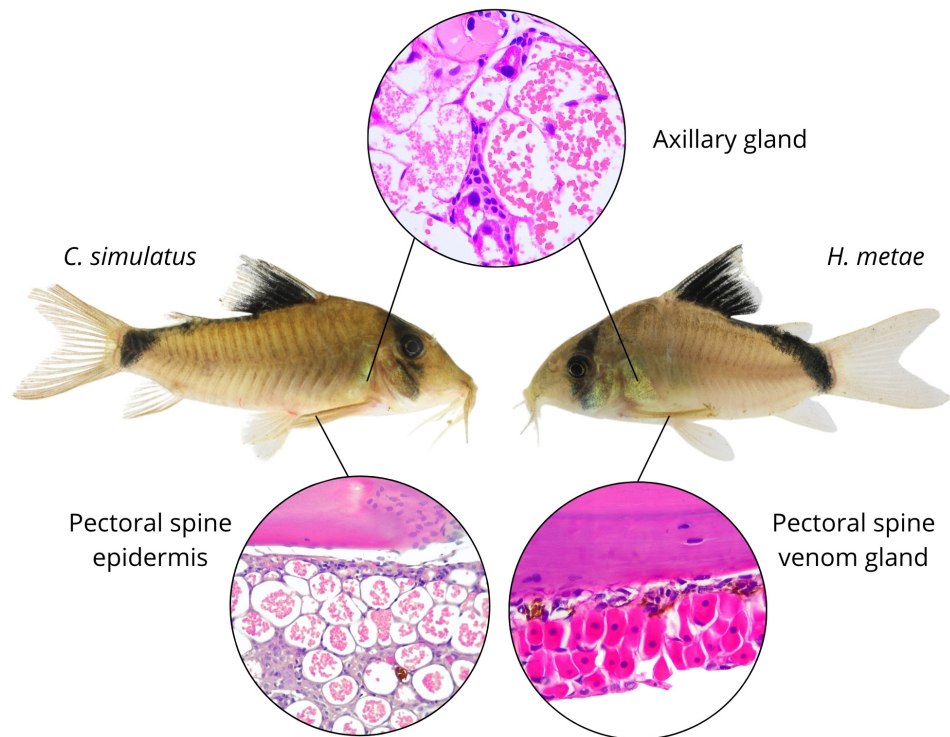


FIGURE 7 | Mimicry ring involving *Corydoras simulatus* and the venomous *Hoplisoma metae* co-occurring in the Meta River basin. Although both possess axillary glands of similar morphology, they differ in the presence of venom spine glands.

Kullander, 2003; Lima, Sazima, 2017). A well-documented case involves *Otocinclus mimulus* Axenrot & Kullander, 2003 and *Hoplisoma diphys* (Axenrot & Kullander, 2003) in the Paraguay basin, where the former is hypothesized to gain protection by mimicking the coloration of the latter. *Hoplisoma diphys* possesses more effective antipredator traits, including a heavily armored body and lockable pectoral and dorsal spines, whereas *O. mimulus* lacks these defenses (Axenrot, Kullander, 2003). A similar pattern was suggested to occur within Corydoradinae itself. Lima, Sazima (2017) proposed that some species of *Corydoras* such as *C. desana* Lima & Sazima, 2017, act as Batesian mimics of species of *Hoplisoma*, such as *H. tukano* (Britto & Lima, 2003). In this case, the unpalatable trait of *H. tukano* is attributed to its sharper, more penetrating pectoral spine, which would release the venom more efficiently in the predator, in contrast to the highly serrated but apparently less pungent spine of *C. desana*. In both scenarios, the more defended species is more frequent than the mimic, allowing the warning signal to remain reliably within the predator community, one of the key conditions for Batesian mimicry. However, because both species retain armored bodies, lockable fin spines, and likely defensive axillary gland secretions, both could be considered defended to some extent. Nevertheless, defensive venoms that result in tissue damage or neurological dysfunction may be required to elicit greater aversion than venoms that cause pain alone (Niermann *et al.*, 2020).

Importantly, our histological analyses reveal clear intergeneric differences in the presence of venom-associated pectoral spine glands, indicating that some genera possess more effective defensive traits than others. Building on these considerations, our results support the existence of mixed mimicry systems within Corydoradinae, in which unequally defended species coexist sympatrically and share similar aposematic color patterns. In this context, the concept of quasi-Batesian mimicry may better explain these interactions. Under this framework, all participating species are defended to some extent, but one species possesses stronger antipredator defenses than the other. As proposed by Speed (1993), quasi-Batesian mimicry occurs when unequally defended species converge on a shared warning signal: both contribute to predator learning through a Müllerian component, while the less defended species may also benefit disproportionately from resembling the more strongly defended model, introducing a Batesian component to the interaction (Speed, 1993; Ruxton *et al.*, 2018).

Consequently, in assemblages with three mimetic species, where two strongly defended coexist with a less defended species exhibiting similar coloration, an interesting case of mixed mimicry ring may arise, in which equally defended taxa participate in Müllerian mimicry while non-equally defended taxa function as quasi-Batesian mimics [e.g., *B. imitator* (Nijssen & Isbrücker, 1983), *H. adolfi* (Burgess, 1982), and *G. nijsseni* (Sands, 1989) in mimicry ring 12 of Alexandrou *et al.*, 2011]. However, quasi-Batesian interactions may shift toward classical Batesian mimicry when predators experience nutritional stress and the less defended species becomes profitable to consume. Under these conditions, the less defended species may function temporarily as a true Batesian mimic, despite retaining some defensive traits (Ruxton *et al.*, 2018).

Incorporating the concept of quasi-Batesian mimicry into the Corydoradinae system suggests that mimicry in this subfamily may represent a continuum between Müllerian and Batesian interactions, raising new questions about the ecological and evolutionary mechanisms underlying these associations. Future studies should evaluate the relative abundance of co-mimetic shoals, the occurrence of polymorphic colour patterns within local assemblages, and predator responses under different nutritional states, as these factors may strongly influence the stability and selective dynamics of mimicry systems.

In conclusion, our study demonstrates that axillary glands are a conserved and structurally consistent feature across Corydoradinae, exhibiting a lobular, holocrine organization comparable to that of other Siluriformes, although their precise functional role remains unresolved and likely multifaceted. In contrast, venom-associated pectoral spine glands show a more restricted phylogenetic distribution, occurring only within a specific clade (*Brochis*, *Hoplisoma*, and *Osteogaster*), which supports a single evolutionary origin of this defensive trait within the subfamily. This heterogeneity in defensive mechanisms has important ecological and evolutionary implications, particularly for mimicry systems, as it challenges the assumption that all Corydoradinae species involved in mimicry rings are equally defended. Instead, our findings support the presence of Müllerian, quasi-Batesian, and Batesian mimicry components within the group, depending on asymmetries in defensive effectiveness among participating taxa, particularly the presence or absence of venom-associated pectoral spine glands.

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Andréa Tonolli Thomaz: Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Writing—review and editing.

Mario Monroy: Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Funding acquisition, Writing—review and editing.

Luiz R. Malabarba: Resources, Investigation, Writing—review and editing.

Angélica J. Garzón-Restrepo: Investigation, Methodology, Writing—review and editing.

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ETHICAL STATEMENT

The experimental procedures involving animals were approved by the Ethics Committee for Animal Experimentation (CEPI) of the Universidad Nacional de Colombia (Approval N° 21688). All fish were euthanized in accordance with the ethical standards and procedures established under Colombian legislation. Specimens collected during fieldwork were obtained under the institutional framework collection permit granted by the Autoridad Nacional de Licencias Ambientales (ANLA) through Resolution N° 255 de 2014, in accordance with Colombian environmental regulations.

DATA AVAILABILITY STATEMENT

All data supporting the findings of this study are available within the article and its supplementary material. Histological photographs underlying the analyses are available from the corresponding author upon request. Examined specimens are deposited in institutional ichthyological collections as indicated in the text.

AI STATEMENT

Grammarly Premium (AI-assisted writing software) was used exclusively for English language editing and grammar correction. The tool was employed only to improve language clarity and readability. It was not used for study design, data analysis, interpretation of results, figure preparation, or the generation of scientific content. All scientific ideas, analyses, and conclusions presented in this manuscript are the original work of the authors.

COMPETING INTERESTS

The authors declare no competing interests.

SUPPLEMENTARY MATERIAL

Supplementary Material File

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