



川陕哲罗鲑鳃组织的显微与超微结构观察

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摘要:【目的】观察分析川陕哲罗鲑鳃组织的显微与超微结构, 丰富其基础生物学资料, 为揭示鱼类鳃组织结构特征与其生活习性的关联提供参考依据。【方法】以人工繁育的川陕哲罗鲑F₁代为研究对象, 采集鳃组织样品分别用4%多聚甲醛和3%戊二醛保存固定, 经石蜡包埋切片后依次进行苏木素—伊红(HE)染色、阿利辛蓝—过碘酸雪夫(AB-PAS)染色、Masson染色及天狼星红染色, 光学显微镜下观察鳃组织学形态、黏液细胞类型、胶原纤维分布与分型; 同时利用扫描电子显微镜和透射电子显微镜观察鳃组织的超微结构。【结果】川陕哲罗鲑有4对鳃, 鳃耙呈乳白色针形, 排列稀疏(12~14根); 鳃丝呈鲜红色, 长条状, 由基部向前端延伸的过程中逐渐变细小, 其末端呈游离状态。鳃弓主要由软骨组织构成, 被覆复层上皮细胞; 鳃丝表面分布有黏液细胞和泌氯细胞, 中央有软骨细胞支撑; 鳃小片由呼吸上皮及柱状上皮组成, 相邻2个柱细胞的胞体延长即围成毛细血管腔, 腔内可见红细胞。AB-PAS染色结果显示, 鳃组织中的黏液细胞以分泌中性黏多糖为主(呈PAS阳性), 伴有少量酸性黏多糖(呈AB阳性)。Masson染色发现, 鳃组织胶原纤维分布均匀, 胶原纤维组织面积占比为0.21%~0.31%(平均为0.27%), 未见纤维化等典型病变。天狼星红染色结果显示, I型胶原纤维的占比为80.00%~90.49%, III型胶原纤维的占比为9.51%~19.20%, I型胶原纤维/III型胶原纤维的比例为4.21~9.51。扫描电子显微镜观察发现, 鳃耙表面凹凸不平且有孔洞, 鳃弓及鳃丝上皮细胞具有密集的环形微嵴, 呈指纹状; 鳃丝表面与鳃小片均有黏液, 但鳃丝表面的孔洞数量多于鳃小片。透射电子显微镜观察发现, 鳃小片主要由扁平上皮细胞、柱细胞、泌氯细胞、巨噬细胞、红细胞、内皮细胞及血管腔中的中性粒细胞等组成, 其中, 泌氯细胞的细胞核呈长椭圆形, 核直径长达约8.3 μm、短径约5.6 μm, 细胞质富含线粒体和粗面内质网。【结论】川陕哲罗鲑的鳃组织结构与其肉食性及高海拔、低水温、急流淡水生境高度适应; 且川陕哲罗鲑鳃组织含有巨噬细胞及中性粒细胞等免疫细胞, 构成其特有的黏膜免疫屏障, 在先天免疫系统中发挥重要作用。

关键词: 川陕哲罗鲑; 鳃; 组织学形态; 黏液细胞; 胶原纤维; 生境适应性

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Microstructure and ultrastructure observation of gill tissue in *Hucho bleekeri*

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Abstract: [Objective] This study aimed to observe and analyze microstructure and ultrastructure of gill tissue in

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Hucho bleekeri and enrich its basic biological data, providing reference for elucidating the association between gill structure characteristics and life habits in fishes. 【Method】The F_1 generation of artificially bred *Hucho bleekeri* was used as the research subject. Gill tissue samples were collected and fixed in 4% paraformaldehyde and 3% glutaraldehyde respectively. After paraffin embedding and sectioning, the samples were sequentially subjected to hematoxylin-eosin (HE) staining, Alcian blue-periodic acid Schiff (AB-PAS) staining, Masson staining, and Sirius red staining. The histological morphology, mucous cell types, and distribution and classification of collagen fibers were observed under a light microscope. Meanwhile, the ultrastructure of gill tissue was examined using scanning electron microscopy and transmission electron microscopy. 【Result】*Hucho bleekeri* possessed four pairs of gills. The gill rakers were milky-white, needle-shaped, and sparsely arranged (12-14 rakers). The gill filaments were bright red and elongated, gradually tapering from the base toward the distal end, with the terminal portion remaining free. The gill arch was primarily composed of cartilaginous tissues and covered by stratified epithelial cells. The gill filament surface was distributed with mucous cells and chloride-secreting cells, with chondrocytes providing central support. The gill lamella consisted of respiratory epithelium and pillar epithelium, and the extended cell bodies of two adjacent pillar cells enclosed the capillary lumen, within which erythrocytes were visible. AB-PAS staining results indicated that mucous cells in gill tissue predominantly secreted neutral mucopolysaccharides (PAS-positive), accompanied by a small amount of acidic mucopolysaccharides (AB-positive). Masson staining revealed that collagen fibers were evenly distributed in gill tissue, with a collagen fiber tissue area proportion of 0.21%-0.31% (the mean was 0.27%), and no typical lesions such as fibrosis were observed. Sirius red staining results showed that type I collagen fibers accounted for 80.00%-90.49%, type III collagen fibers accounted for 9.51%-19.20%, and the ratio of type I/type III collagen fibers ranged from 4.21 to 9.51. Scanning electron microscopy observation revealed that the gill raker surface was uneven and porous; the epithelial cells of gill arches and filaments possessed dense circular microridges arranged in a fingerprintlike pattern; mucus was found on both gill filament surface and gill lamellae, but the number of pores on gill filament surface exceeded that on the gill lamellae. Transmission electron microscopy observation revealed that the gill lamella was mainly composed of flattened epithelial cells, pillar cells, chloride-secreting cells, macrophages, erythrocytes, endothelial cells, and neutrophils in the vascular lumen. Among these, the chloride-secreting cells had an elongated oval nucleus, with the long diameter at 8.3 μm and short diameter at 5.6 μm approximately, and the cytoplasm had abundant mitochondria and rough endoplasmic reticulum. 【Conclusion】The gill tissue structure in *Hucho bleekeri* is highly adapted to its carnivorous nature and the habitat of high altitude, low temperature, and fast-flowing freshwater. Moreover, the gill tissue of *Hucho bleekeri* have immune cells such as macrophages and neutrophils, constituting a specific mucosal immune barrier that plays an important role in innate immune system.

Key words: *Hucho bleekeri*; gill; histological morphology; mucous cell; collagen fiber; habitat adaptability

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0 引言

【研究意义】川陕哲罗鲑(*Hucho bleekeri*)隶属于鲑形目(Salmoniformes)鲑科(Salmonidae)哲罗鲑属(*Hucho*)(丁瑞华, 1995),为国家一级重点保护野生动物,已被世界自然保护联盟(IUCN)列为极危级(CR)物种,是哲罗鲑属鱼类中分布最靠南的种类(Rand, 2013)。川陕哲罗鲑是我国长江上游的旗舰物种,为肉食性鱼类(周仰璟和吴万荣, 1990),通常分布在海拔2690~3598 m的水域环境(河底多石,水流湍急,流速和水深多变),其适宜水温为4~14 $^{\circ}\text{C}$ (周仰璟和吴万荣, 1987; 丁瑞华, 1995; 茹辉军等, 2015)。因其独特的生物学特征及栖息环境,导致川陕哲罗鲑的分布范围极窄,仅分布于长江水系的大渡河、岷江及汉江水系(申志新等, 2005; 杜浩等, 2014; 茹辉军等, 2015)。受梯级水电开发等因素的影响,川陕哲罗鲑栖息地的水温、急流等环境因子发生剧变,目前在大渡河流域其生境损失量高达91.4%(茹辉军等, 2015),通过密度法估算出的太白河川陕哲罗鲑现存资源量仅为3814尾(屈万民等,

2024)。栖息环境的剧变及野生资源量的锐减,可能会导致川陕哲罗鲑灭绝,因此亟需强化川陕哲罗鲑基础生物学研究,为制定科学有效的保护策略及种群恢复方案提供理论支撑,从而切实降低川陕哲罗鲑野外灭绝的风险。【前人研究进展】鳃是鱼类与水生环境的重要连接,在呼吸、渗透压调节及酸碱平衡调控方面发挥着关键作用(Chen et al., 2023; Gilmour and Turko, 2024; Kovac and Goss, 2024; Pan, 2024)。鱼鳃表面积大且直接与外界水环境相通,对水体中微小的理化变化十分敏感,也是各种水体污染物主要作用的靶器官(Mir and Channa, 2009; 林欣等, 2024),因此通过观察鳃组织形态变化,可评判鱼类的健康状况及水体的污染程度(Strzyzewska et al., 2016),尤其适用于判定各类环境因子诱发的鱼类病害(Mitchell and Rodger, 2011)。鳃组织具有非常复杂、精妙的结构(Wilson and Laurent, 2002),与气体交换、渗透压调节、氮代谢废物排泄及离子平衡维持等功能密切相关(Perna and Fernandes, 1996),但不同鱼类鳃组织的形态结构存在明显差异(方静等,

2004; 向乾乾等, 2018; Hanafy, 2020; 葛玉腾等, 2024), 与鱼类对环境的适应性具有复杂关联 (Zydlewski and McCormick, 2001; 赵峰等, 2016; Schnell et al., 2016)。Abdel-Hameed等(2026)通过多种组织染色方法对鲢(*Hypophthalmichthys molitrix*)的鳃骨骼进行系统显微解剖学分析, 结果发现鳃弓主要由成熟骨组织构成, 软骨细胞外基质富含酸性黏多糖、蛋白质与糖蛋白等, 能为细胞代谢活动提供充足的能量。从解剖层面来看, 鳃组织的血管形态多样, 与其多样化的生理功能相适应; 鳃组织特有的柱细胞构成呼吸性血管壁内层, 对循环激素发挥重要代谢调控作用 (Olson, 1991; 廖嘉仪等, 2024)。Cinar等(2009)研究证实, 在安塔利亚拟鲃(*Pseudophoxinus antalyae*)鳃上皮的扁平上皮细胞间散在分布有黏液细胞, 且绝大多数黏液细胞着色呈紫色, 含有硫酸化糖复合物及羧基化糖复合物。Sackville等(2024)研究发现, 鱼类鳃部离子调节功能的起源远早于气体交换功能, 原始咽鳃弓的离子调节机制在鱼类的滤食生理活动中发挥重要作用, 后续在脊椎动物演化进程中还承担细胞外液离子稳态维持与酸碱平衡调控的生理作用。Alsafy等(2025)研究发现, 鳃耙的长短及形态主要与鱼类的食性密切相关, 多数鱼类的外侧鳃耙较内侧鳃耙更长、数量更多、发育更完善。此外, 通过鳃组织形态的变化可评判鱼类所处的环境状态。Santos等(2019)研究表明, 不同鱼类对水环境胁迫的应答反应存在明显物种差异, 鳃丝与鳃小片上皮增生病变能较好地反映河流生态等级, 即该指标适用于水域生态生物监测。【本研究切入点】川陕哲罗鲑为濒危保护物种, 位于产区水生生物的能量终端和食物链顶端(吴万荣, 1989; 丁瑞华, 1995; 茹辉军等, 2015), 针对其基础生物学的研究报道较多, 包括食性与食物消化(周仰璟和吴万荣, 1990)、鳞片结构(丁瑞华和方盛国, 1995)、精子形态结构(郭威等, 2016)、早期发育形态学(杨焕超等, 2016)、遗传结构(Chen et al., 2018)及其免疫机理(Chen et al., 2021)等, 但尚无鳃组织结构的相关报道, 其与环境的适应性也尚未明确。【拟解决的关键问题】通过光学显微镜、扫描电子显微镜及透射电子显微镜观察分析川陕哲罗鲑鳃组织的显微与超微结构, 丰富其基础生物学资料, 为揭示鱼类鳃组织结构特征与其生活习性的关联提供参考依据。

1 材料与方法

1.1 试验材料

人工繁育的川陕哲罗鲑F₁代由四川省农业科学院水产研究所(四川省水产研究所)提供, 其体质量

为230±15 g, 体长为25.01±1.22 cm。川陕哲罗鲑在实验室条件下暂养2周, 暂养期间保持充气增氧, 水体溶解氧含量>6.0 mg/L, pH 7.0±0.2。以100 mg/L的MS-222麻醉后采集川陕哲罗鲑的鳃组织样品, 分别用4%多聚甲醛和3%戊二醛进行固定保存。动物试验由四川省农业科学院水产研究所(四川省水产研究所)动物伦理与福利委员会审查批准, 批准号20230927002A。

1.2 鳃组织学形态观察

4%多聚甲醛固定的鳃组织样品经流水冲洗后, 进行脱钙及组织修块, 再放入病理包埋塑料筐中进行脱水(75%乙醇6 h, 85%乙醇10 h, 95%乙醇4 h, 无水乙醇I 2 h, 无水乙醇II 2 h); 然后用二甲苯分别透明处理20和15 min, 浸蜡3 h, 包埋组织块于石蜡中。采用切片机将组织切成5 μm的超薄切片, 在温水中将组织切片展平后捞片, 60℃烘烤组织切片至少2 h; 经二甲苯脱蜡后流水洗涤20 min, 苏木素染色30 min, 流水洗涤20 min, 盐酸乙醇分化, 伊红染色5 min; 经梯度乙醇脱水及二甲苯透明后以中性树胶封片。在光学显微镜下观察鳃组织学形态, 并通过显微成像系统采集图像。

1.3 鳃组织黏液细胞阿利辛蓝—过碘酸雪夫(AB-PAS)染色

鳃组织切片完成脱蜡后, 采用阿利辛蓝染液染色10~20 min, 蒸馏水漂洗3次, 每次1~2 min; 随后置于氧化剂中氧化5~8 min, 自来水冲洗, 再以蒸馏水浸洗2次; 将组织切片浸入Schiff's试剂中浸染10~20 min, 弃除染液后使用蒸馏水漂洗2次, 每次5 min; 经梯度乙醇脱水及透明剂透明处理后, 使用中性树胶封片。

1.4 鳃组织Masson染色

鳃组织切片完成脱蜡后, 使用重铬酸钾过夜孵育; 然后将组织切片放入63℃烘箱烘烤1 h, 以丽春红品红染色液染色10 min, 蒸馏水稍冲洗; 磷钼酸溶液处理至胶原纤维褪色; 苯胺蓝染色约2 min, 经梯度乙醇脱水及透明剂透明处理后, 使用中性树胶封片。

1.5 鳃组织天狼星红染色

鳃组织切片完成脱蜡后, 以苏木素染色并吹干切片, 再以天狼星红复合染色液染色5~10 min; 正丁醇脱水5 min, 然后梯度乙醇脱水, 透明剂透明, 并以中性树胶封片。

1.6 扫描电子显微镜观察鳃组织超微结构

鳃组织样品经3%戊二醛固定后水洗3次, 每次10 min; 再以1%四氧化锇后固定1 h, 水洗3次, 每

次 10 min; 梯度乙醇脱水(30%→50%→70%→80%→90%→95%→100%, 其中 100% 换 3 次), 每次 15 min。鳃组织样品经临界点干燥后, 用导电胶黏于样品座上, 经离子溅射喷镀处理后, 通过扫描电子显微镜观察鳃组织超微结构。

1.7 透射电子显微镜观察鳃组织超微结构

鳃组织样品依次进行 3% 戊二醛预固定、1% 四氧化锇后固定及梯度丙酮脱水(30%→100%, 100% 换 3 次); 按丙酮:Epon-812 为 3:1、1:1、1:3 进行梯度渗透后, 纯包埋剂包埋过夜; 半薄切片光镜定位, 超薄切片(60~90 nm)使用铜网捞网, 然后在室温下以醋酸铀染色 10~15 min、柠檬酸铅染色 1~2 min。通过透射电子显微镜对铜网进行图像采集, 每张铜网先在低倍镜下观察全部组织, 再选择要观察的区域采集图像。

2 结果与分析

2.1 川陕哲罗鲑鳃组织的一般形态结构

川陕哲罗鲑鳃组织的一般形态结构与其他硬骨鱼类基本相似, 位于咽部后端两侧(图 1-A), 具有 4 对鳃, 且 4 对鳃的长度依次缩短, 主要由鳃丝、鳃耙、鳃弓和鳃小片构成。鳃耙和鳃弓呈乳白色, 鳃耙位于鳃弓内侧, 每个鳃弓的内侧仅有一列鳃耙; 鳃耙排列稀疏, 通常有 12~14 根, 呈针形, 相邻鳃耙间的间隙清晰(图 1-B)。鳃小片由许多平行排列的长条状鳃丝构成, 鳃丝呈鲜红色, 长条状; 鳃丝由基部向前端延伸的过程中逐渐变细小, 其基部稳固在鳃弓的外侧凸面, 末端呈游离状, 整个鳃瓣呈梳状(图 1-C)。

2.2 川陕哲罗鲑鳃组织光学显微镜观察结果

川陕哲罗鲑鳃组织由鳃弓、鳃耙、鳃丝和鳃小片组成。鳃弓主要由软骨组织构成, 被覆复层上皮细胞; 鳃丝表面有上皮细胞, 上皮细胞下分布有黏液细胞和泌氯细胞, 中央有软骨细胞支撑, 呈圆形或椭圆形; 两侧可见多个鳃小片, 鳃小片由呼吸上皮和柱状上皮组成, 相邻 2 个柱细胞的胞体延长即围成毛细血管腔; 鳃小片可见毛细血管, 且毛细血管内可见红细胞(图 2)。低倍镜下, 可见从鳃弓延伸出的鳃丝呈梳状排列, 鳃丝向两侧延伸出呈半圆形扁平的鳃小片(图 2-A)。高倍镜下, 观察到鳃丝中轴有蓝染的软骨细胞; 鳃小片由大量的扁平上皮细胞(呼吸上皮细胞)组成; 部分鳃小片卷曲, 鳃小片上皮细胞与鳃丝上皮相连, 呈扁平状(图 2-B)。

2.3 川陕哲罗鲑鳃组织黏液细胞分析结果

通过 AB-PAS 染色检查川陕哲罗鲑鳃组织中黏液细胞的阳性表达情况, 结果(图 3)显示, 黏液细胞主要定位于鳃上皮表层, 沿鳃丝的游离面分布。大部分黏液细胞呈紫红色, 同时有少量蓝紫色的黏液细胞, 说明川陕哲罗鲑鳃组织中的黏液细胞同时呈 PAS 阳性(PAS+)和 AB 阳性(AB+)。此外, AB-PAS 染色后的紫红色黏液细胞居多, 说明这些黏液细胞主要分泌中性黏多糖及少量酸性黏多糖。

2.4 川陕哲罗鲑鳃组织胶原纤维分析结果

川陕哲罗鲑鳃组织经 Masson 染色后, 可观察到胶原纤维呈蓝色, 而肌纤维、胞质和红细胞等呈不同程度的红色(图 4)。在鳃丝中央的结缔组织及鳃小片间的基底膜, 可见清晰的蓝色胶原纤维沉积, 且胶

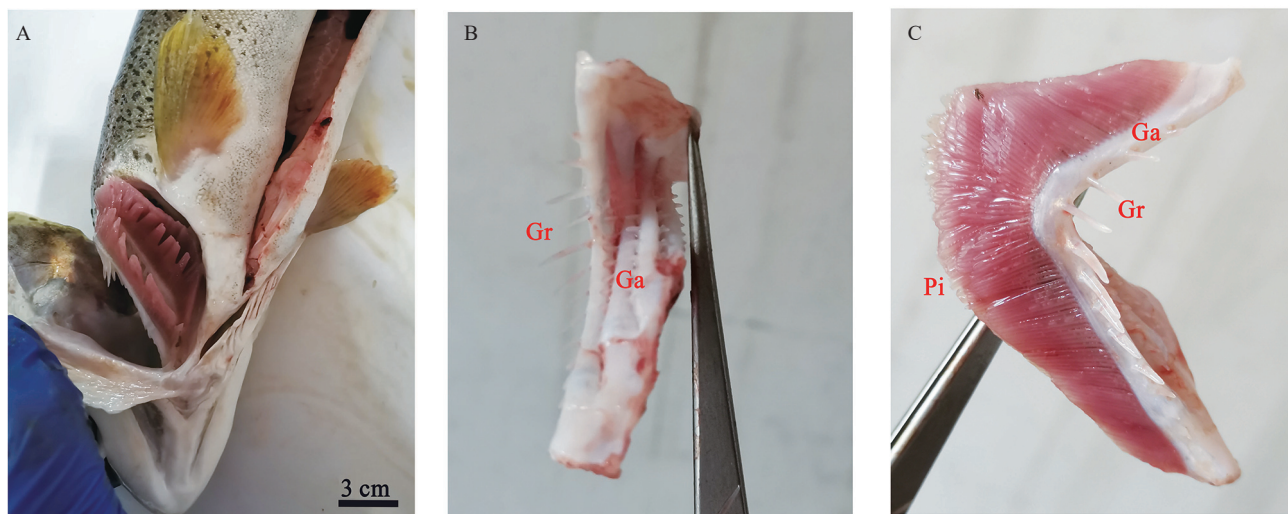


图 1 川陕哲罗鲑鳃组织的解剖学结构

Fig. 1 Anatomical structure of gill tissue in *Hucho bleekeri*

Ga: 鳃弓; Gr: 鳃耙; Pi: 鳃丝

Ga: Gill arch; Gr: Gill raker; Pi: Gill filament

原纤维分布均匀,无异常增生或大量纤维化聚集。通过计算不同视野下胶原纤维的面积,发现川陕哲罗鲑鳃组织内的胶原纤维面积占比为0.21%~0.31%,平均为0.27%。鳃丝中央的血管内可见红染的红细胞,血管壁结构完整,无明显充血现象。

2.5 川陕哲罗鲑鳃组织胶原纤维分型分析结果

川陕哲罗鲑鳃组织经天狼星红染色后,在偏振光显微镜下观察发现I型胶原纤维呈亮黄色或红色,III型胶原纤维呈绿色(图5)。川陕哲罗鲑鳃组织中存在丰富的I型胶原纤维及少量的III型胶原纤维,其

中,I型胶原纤维的占比为80.00%~90.49%,III型胶原纤维的占比为9.51%~19.20%,I型胶原纤维/III型胶原纤维的比例为4.21~9.51。

2.6 川陕哲罗鲑鳃组织扫描电子显微镜观察结果

川陕哲罗鲑鳃耙表面凹凸不平,具有许多呈不规则或椭圆形的孔洞,孔洞长径为4.6~8.6 μm;鳃耙表面为单层上皮细胞,环形微嵴类似于迷宫,形成指纹状的纹路,细胞间分界不明显(图6)。鳃弓表面具有许多褶皱,且褶皱方向保持一致,其表面可见多边形的上皮细胞和微脊。单层上皮细胞呈中部低、周

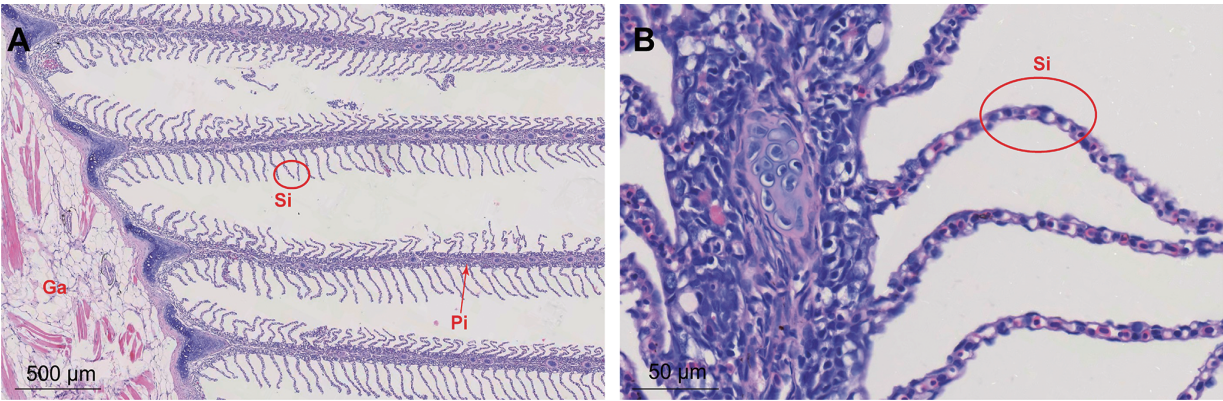


图2 川陕哲罗鲑鳃组织的光学显微镜观察结果

Fig. 2 Light microscope observation results of gill tissue in *Hucho bleekeri*

A: 鳃纵切面;B: 鳃小片切面。Ga: 鳃弓;Pi: 鳃丝;Si: 鳃小片

A: Longitudinal section of gill; B: Cross section of gill lamella. Ga: Gill arch; Pi: Gill filament; Si: Gill lamella

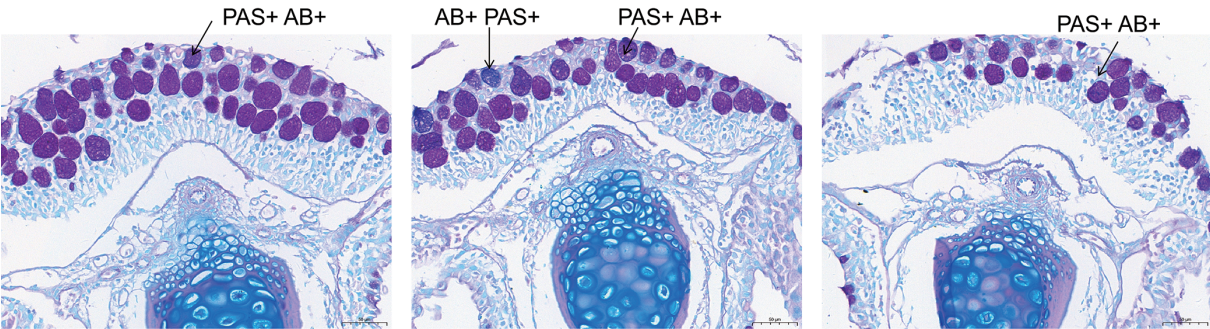


图3 川陕哲罗鲑鳃组织黏液细胞的AB-PAS染色结果

Fig. 3 AB-PAS staining results of mucous cells of gill tissue in *Hucho bleekeri*

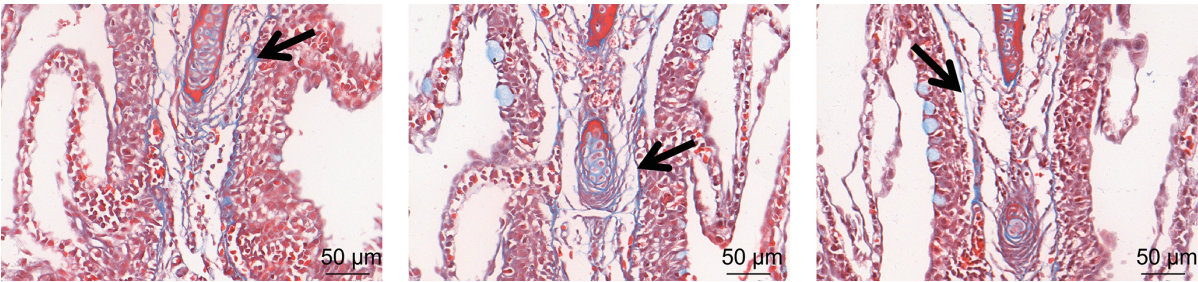


图4 川陕哲罗鲑鳃组织胶原纤维的Masson染色结果

Fig. 4 Masson staining results of collagen fibers of gill tissue in *Hucho bleekeri*

箭头所指为胶原纤维

Arrows represented collagen fibers

围高,细胞直径为65.0~84.0 μm 。上皮细胞间存在微小孔,为黏液细胞开口处,部分孔洞内有块状的分泌物。川陕哲罗鲑的鳃丝末端类似于香蕉尾部,鳃丝末端和鳃丝中部表面均由单层上皮细胞覆盖,单层上皮细胞的环形微嵴非常密集,呈指纹状,各细胞形状差异明显。鳃丝表面与鳃小片相似,有黏液,但鳃丝表面的孔洞数量多于鳃小片。

2.7 川陕哲罗鲑鳃组织透射电子显微镜观察结果

川陕哲罗鲑的鳃小片主要由扁平上皮细胞、柱细胞、泌氯细胞、巨噬细胞、红细胞、内皮细胞及血管腔中的中性粒细胞等组成。泌氯细胞的细胞核呈长椭圆形,核直径长边约8.3 μm 、短边约5.6 μm ,染色质分布均匀,以常染色质为主,异染色质少,核膜连续完整;细胞质中可见大量线粒体和粗面内质网,大部分线粒体轻度肿胀,呈杆状或圆形,嵴少量断裂、溶解,基质部分溶解、电子密度降低,外膜连续完整;粗面内质网轻度扩张,囊腔间隙轻微增宽,胞质面附着核糖体颗粒;细胞浆中可见囊泡(图7)。鳃小片基部多见泌氯细胞,其细胞质富含线粒体与内质网,还可见柱细胞和内皮细胞。其中,柱细胞的细胞核呈圆形,直径约5.8 μm ;内皮细胞的细胞核呈长椭圆形,核直径长边约2.9 μm 、短边约1.9 μm ,线粒体以圆形为主,偶见椭圆形或弯曲杆状。

3 讨论

鳃组织在所有鱼类中均发挥着多种功能,其中,第一个重要功能是鱼类进行气体交换的主要场所(葛玉腾等,2024),第二个功能与摄食习性有关,如鳃丝的排列能反映鱼类的摄食习惯(Kumari et al., 2009; Elsheikh, 2013)。弓形结构的鳃弓既可稳固鳃丝排布形态,又能减缓湍急水流的流速。鳃弓内侧的鳃耙是重要的滤食结构,如黄颡鱼(*Pelteobagrus fulvidraco*)(罗芬等,2011)、怒江裂腹鱼(*Racoma gongshanensis*)(向乾乾等,2018)等鱼类的

鳃耙细长,排列稀疏。本研究观察发现,川陕哲罗鲑鳃组织上存在一定数量的黏液细胞,经AB-PAS染色证实其主要分泌中性黏多糖。鲑科鱼类鳃组织糖蛋白类型具有显著的环境可塑性,生活在淡水中的大西洋鲑(*Salmo salar*)、褐鳟(*Salmo trutta*)及虹鳟(*Oncorhynchus mykiss*),其鳃部黏液细胞以中性黏多糖PAS+占优势,若在海水环境中则转变为以酸性黏多糖AB+为主(Roberts and Powell, 2005)。川陕哲罗鲑为典型的淡水定居型鲑科鱼类,其鳃组织的黏液细胞以中性黏多糖为主,是对淡水低渗环境的适应性表现。此外,中性黏多糖形成黏液凝胶层的黏度较低,有利于维持鳃小片表面的层流,减少水流阻力与氧气扩散屏障,从而保障呼吸效率(Riera-Ferrer et al., 2024)。鳃小片作为气体交换的主要场所,其表面的黏液层不宜过于黏稠,否则将阻碍气体扩散与水流通过。AB-PAS染色发现,川陕哲罗鲑鳃组织中的黏液细胞也分泌少量的酸性黏多糖。酸性黏多糖对上皮组织具有保护作用(Ni et al., 2025),其末端通常含有唾液酸等带负电荷的残基,能抵抗细菌分泌降解酶的破坏,提升黏膜屏障抵御病原入侵及遏制微生物感染的能力(Riera-Ferrer et al., 2024)。因此,川陕哲罗鲑鳃组织的黏液细胞呈典型的III型特征,即大量中性黏多糖中混杂有少量酸性黏多糖,反映了呼吸功能优先、免疫防御兼顾的生理平衡。

鳃组织纤维化程度是判断其病理状态的重要指标之一。Masson染色发现,川陕哲罗鲑鳃组织的胶原纤维分布与染色强度正常,未见纤维化(胶原过度增生、大片蓝染)等典型病变,说明川陕哲罗鲑的鳃组织无明显病理损伤。此外,胶原纤维仅在正常的结缔组织区域分布,无病理性增生,提示川陕哲罗鲑鳃组织的结缔组织支持结构未发生异常重塑。该结论为判断川陕哲罗鲑鳃组织是否发生病理损伤提供了正常组织形态学参考样本。天狼星红染色进一步

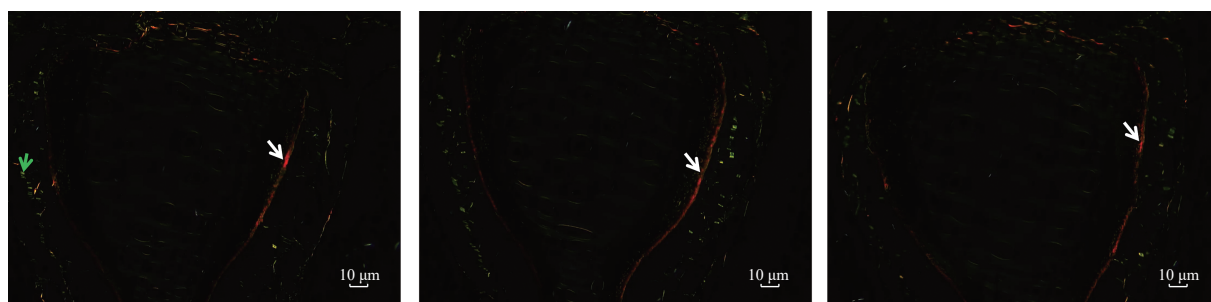


图5 川陕哲罗鲑鳃组织的天狼星红染色结果

Fig. 5 Sirius red staining results of gill tissue in *Hucho bleekeri*

白色箭头所指为I型胶原纤维;绿色箭头所指为III型胶原纤维

White arrows represented type I collagen fiber; green arrows represented type III collagen fiber

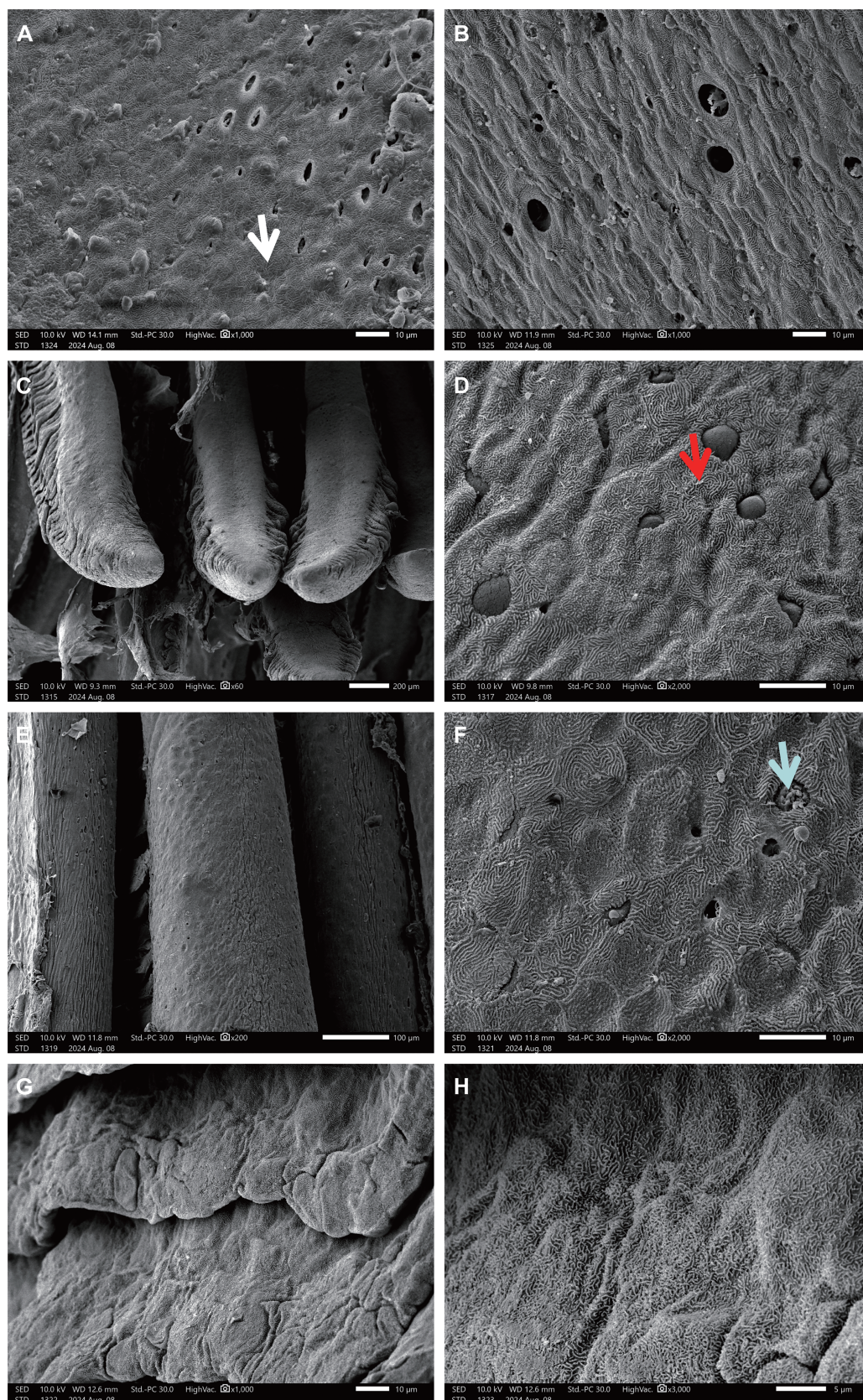


图6 川陕哲罗鲑鳃组织的扫描电子显微镜观察结果

Fig. 6 Scanning electron microscope observation results of gill tissue in *Hucho bleekeri*

A: 鳃耙; B: 鳃弓; C: 鳃丝顶端; D: 鳃丝顶端局部放大; E: 鳃丝中部; F: 鳃丝中部局部放大; G: 鳃小片; H: 鳃小片局部放大。

白色箭头所指为扁平上皮细胞, 红色箭头所指为微脊, 蓝色箭头所指为黏液细胞开口处的分泌物

A: Gill raker; B: Gill arch; C: Gill filament tip; D: Enlarged gill filament tip; E: Middle gill filament; F: Enlarged middle gill filament; G: Gill lamella; H: Enlarged gill lamella. White arrows represented flattened epithelial cells, red arrows represented microridges, and blue arrows represented secretions at openings of mucous cells

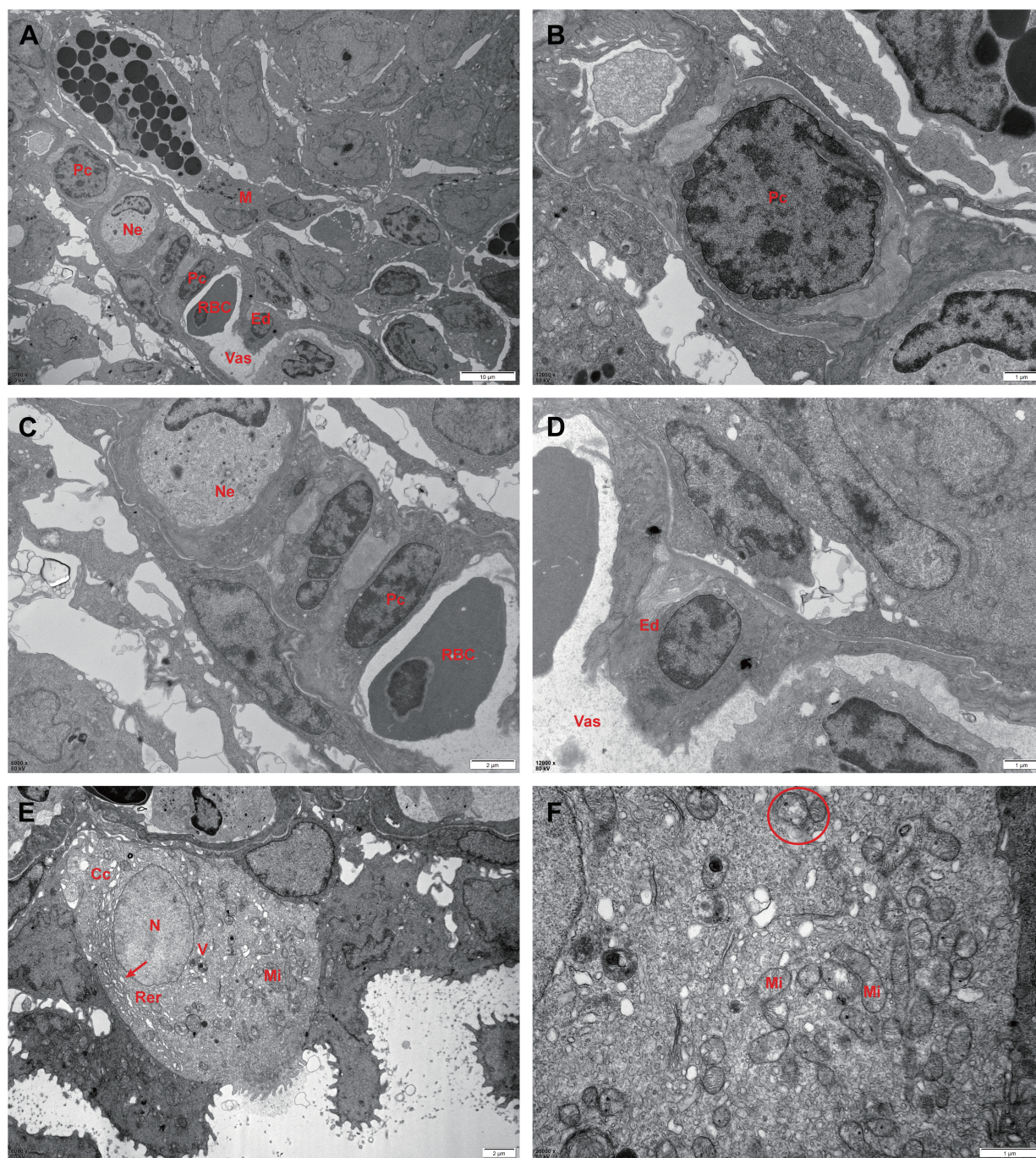


图7 川陕哲罗鲑鳃组织的透射电子显微镜观察结果

Fig. 7 Transmission electron microscope observation results of gill tissue in *Hucho bleekeri*

A: 鳃小片结构组成; B: 柱细胞结构; C: 中性粒细胞结构; D: 内皮细胞结构; E: 泌氯细胞结构; F: 线粒体结构。Ed: 内皮细胞; M: 巨噬细胞; Mi: 线粒体; N: 细胞核; Ne: 中性粒细胞; Pc: 柱细胞; RBC: 红细胞; Rer: 粗面内质网; V: 囊泡; Vas: 血管腔; 箭头: 粗面内质网扩张; 红圈: 线粒体轻度肿胀

A: Structural composition of gill lamella; B: Structure of pillar cell structure; C: Structure of neutrophil; D: Structure of endothelial cell; E: Structure of chloride-secreting cell; F: Structure of mitochondrion. Ed: Endothelial cell; M: Macrophage; Mi: Mitochondrion; N: Nucleus; Ne: Neutrophil; Pc: Pillar cell; RBC: Erythrocyte; Rer: Rough endoplasmic reticulum; V: Vesicle; Vas: Vascular lumen; Arrow: Dilated rough endoplasmic reticulum; Red circle: Mild swelling of mitochondrion

揭示川陕哲罗鲑鳃组织具有相对丰富的I型胶原纤维及少量的III型胶原纤维。I型胶原纤维几乎分布在所有细胞外基质与结缔组织中,而III型胶原纤维多存在于皮肤、血管及各类脏器组织中(Amirrah et al., 2022)。I型胶原纤维在皮肤及骨骼组织中发挥

核心生理功能,同时有少量分布在其他组织的细胞外基质内(Henriksen and Karsdal, 2016)。鱼类的软骨结构通常呈现一定多样性,如花鲈(*Poecilia sphe-nops*)存在5种不同的软骨类型,草鱼(*Ctenopharyn-godon idella*)和锯盖足鲈(*Sphaerichthys osphrome-*

noides)在下颌半月板中还存在1种额外的软骨类型——纤维/细胞丰富型软骨,其特征为软骨基质中含有高密度的胶原纤维(Mokhtar et al., 2025)。川陕哲罗鲑鳃组织中I型胶原纤维占比较高,即I型胶原纤维在鳃丝中央轴形成的致密纤维束为血管和上皮组织提供了刚性支撑。III型胶原纤维在动物发育阶段高表达,与I型胶原纤维协同表达并形成异型胶原纤维,还能调控胶原纤维直径(Fleischmajer et al., 1990)。Lin等(1997)研究证实,敲除III型胶原纤维基因(*COL3A1*)会引起小鼠皮肤的真皮层与主动脉外膜中胶原纤维粗细不均。由此推测,少量III型胶原纤维对鳃组织胶原纤维的尺寸与直径起调控作用。

鱼类鳃上皮包含表层扁平细胞、氯细胞、黏液细胞及基底上皮细胞等多种细胞类型;鳃弓上皮存在淋巴间隙,而间隙内分布有淋巴细胞、颗粒白细胞等免疫细胞(Alsafy et al., 2025)。其中,上皮细胞具有保护、离子吸收、气体交换及酸碱平衡调节等功能(Wilson et al., 2000; Evans et al., 2005),不同鱼类的鳃上皮细胞形态不一(向乾乾等, 2018),与其生活习性密切相关。相对于其他冷水性鱼类,川陕哲罗鲑鳃上皮细胞的微嵴较多、直径更大,增大了鳃组织的表面积,有效提高了川陕哲罗鲑在急流环境中的气体交换率(Evans et al., 2005)。川陕哲罗鲑的鳃丝由数量众多的鳃小片组成,而鳃小片上的上皮细胞排列紊乱,具有微脊和分泌孔等,有利于气体交换与离子吸附,与虹鳟(Morgan, 1974)、齐口裂腹鱼(*Schizothorax prenanti*)(方静等, 2004)、草鱼(孙京田和周茂新, 2004)、黄颡鱼(罗芬等, 2011)、怒江裂腹鱼(向乾乾等, 2018)等鱼类的鳃丝结构相似。川陕哲罗鲑的鳃小片主要由扁平上皮细胞构成,进一步验证了鳃组织的呼吸功能。此外,透射电子显微镜观察发现川陕哲罗鲑鳃组织中含有一定数量、不同类型的免疫细胞,包括中性粒细胞和巨噬细胞等。鳃是硬骨鱼类与外界水环境进行气体交换的主要器官,其表面积巨大,也是病原体入侵的首选靶器官。因此,鳃组织必须具备完整的先天免疫防御体系,通过各类固有免疫、适应性免疫细胞及免疫分子协同作用,共同抵御病原微生物的侵袭(Gomez et al., 2013)。巨噬细胞和中性粒细胞作为先天性免疫的核心效应细胞(Silva, 2010),是鳃黏膜防御的第一道细胞屏障,对病原微生物起清除作用。

4 结论

川陕哲罗鲑的鳃耙稀疏呈针形,鳃组织的黏液细胞以中性黏多糖为主,胶原纤维分布正常且以I型

胶原纤维为主,鳃丝上皮细胞的环形微嵴非常密集,即川陕哲罗鲑的鳃组织结构与其肉食性及高海拔、低水温、急流淡水生境高度适应。此外,川陕哲罗鲑鳃组织含有巨噬细胞及中性粒细胞等免疫细胞,构成其特有的黏膜免疫屏障,在先天免疫系统中发挥重要作用。

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