

## 中华乌塘鳢嗅觉器官的形态结构

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**摘要:**中华乌塘鳢(*Bostichthys sinensis* Lacepede)标本体长17.0~19.8 cm,性成熟鱼性腺为IV~V期,性未成熟鱼性腺为II期。取嗅囊切片、染色、固定。分别以扫描电镜和透射电镜拍照。结果显示,中华乌塘鳢具一对纺锤形嗅囊,由前、后鼻孔与外界相通,嗅上皮向嗅囊腔内突起形成10~16个初级嗅板,初级嗅板上有次级嗅板,可增大嗅上皮的表面积。嗅板由嗅上皮和中央髓两部分构成,中央髓主要由疏松结缔组织和毛细血管构成;嗅上皮排列于中央髓的两侧,由多层细胞组成。扫描和透射电镜观察表明:嗅上皮分为非感觉区和感觉区两部分,非感觉区位于嗅板边缘,较薄且平滑,外缘高倍放大呈指纹状或块状结构;感觉区位于中央部位,呈连续分布,细胞种类多样,表层为纤毛非感觉细胞,中上层为纤毛感受细胞和柱状细胞,中下层为支持细胞,底层为基底细胞。纤毛感受细胞为一种双极神经元,树突在上皮表面形成嗅结;轴突则穿过基膜,在固有层内集合成束,形成嗅神经纤维,终止于嗅叶。

**关键词:**中华乌塘鳢;嗅觉器官;形态结构

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鱼类嗅觉器官是一种远距离化学感受器,敏感性极高,它对于鱼类的觅食、识别、集群、求偶、洄游、防御敌害等均有重要意义<sup>[1]</sup>。中华乌塘鳢(*Bostichthys sinensis* Lacepede)栖息于沿海河口潮间带滩涂<sup>[2]</sup>,生殖季节成熟雌、雄鱼择偶配对进入洞穴内交配产卵,嗅觉在其生殖过程中起重要作用。作者曾以嗅电图(EOG)方法研究了中华乌塘鳢嗅上皮对性外激素刺激反应的敏感性,结果表明,性成熟中华乌塘鳢对不同种类的性外激素刺激所产生的EOG是有差异的<sup>[3]</sup>。有关中华乌塘鳢嗅觉器官形态结构的研究,国内外尚未见文献报道。本研究旨在通过观察中华乌塘鳢嗅觉器官的外部形态以及显微和超微结构,以探明其嗅觉对性外激素的反应机理。

### 1 材料与方法

中华乌塘鳢取自农贸市场,体长17.0~19.8 cm,体重98.4~114.5 g,性成熟鱼性腺为IV~V期,性未成熟鱼性腺为II期。剪开中华乌塘鳢前后鼻孔之间的皮肤,暴露嗅囊并迅速取出,Bouin氏液固定,石蜡包埋,切片厚度6 μm,HE染色,Olymp-

lus DX51 显微镜观察拍照。另以2.5%戊二醛和1%锇酸双重固定,干燥喷金后在Philips XL30ESEM扫描电镜下观察拍照;环氧树脂(618号)包埋,切片后柠檬酸铅复染,JEM-100CXⅡ透射电镜下观察拍照。

### 2 结果与分析

#### 2.1 嗅觉器官的形态

中华乌塘鳢的嗅囊位于头部两侧的鼻腔内,经前鼻孔和后鼻孔与外界相通。前鼻呈小管状突起并延伸至上颌前方边缘,后鼻为一较宽的短管,后鼻孔呈椭圆形,位于眼球的侧前方。中华乌塘鳢的嗅觉器官已发育成嗅囊,呈纺锤形。剖开嗅囊,可见初级嗅板由嗅囊壁向腔内突起,呈平行排列,方向与鼻腔的长径一致(图版1-1)。

#### 2.2 嗅觉器官的显微和超微结构

在光镜下,从中华乌塘鳢嗅囊的横切面可见,嗅上皮向嗅囊腔内突起形成初级嗅板,较大的初级嗅板上有次级嗅板,为不同形状、大小的皱褶突起。每个嗅囊由10~16个初级嗅板组成,嗅板向嗅囊腔内突起的高度不一,从腹部正中伸出的一个初级嗅板

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最高,可伸至腔的对侧(图版I-2)。嗅板由嗅上皮和中央髓两部分构成,中央髓位于嗅板的中央腔内,由网状纤维、胶原纤维等疏松结缔组织和大量的毛细血管构成(图版I-3);嗅上皮排列于中央髓两侧,细胞分层明显,主要由纤毛非感觉细胞、纤毛感受细胞、支持细胞、基细胞组成(图版I-4)。

在扫描电镜下,可见中华乌塘鳢的单个嗅板呈叶片状(图版I-5),图1为扫描电镜下嗅板的细胞分区示意图,嗅上皮由边缘非感觉区和中央感觉区组成。非感觉区位于嗅板边缘,靠近嗅板基部的边缘为指纹状嵴结构,由众多凸起的嵴环绕而成,嵴上有小孔,嵴的表面或间隙有小泡状分泌物(图版I-6);伸向嗅囊腔的边缘呈块状嵴结构,嵴的表面或间隙也有小泡状分泌物(图版I-7);指纹状嵴和块状嵴内侧是由众多纤毛非感觉细胞组成的非感觉区,细胞的纤毛朝同一方向弯曲(图版I-8)。感觉区位于嗅板的中央部位,呈连续分布,细胞种类多样,由纤毛非感觉细胞、纤毛感受细胞、柱状细胞和支持细胞组成。

光镜和电镜观察表明,嗅上皮主要由5种细胞构成,即纤毛非感觉细胞、纤毛感受细胞、柱状细胞、支持细胞和基细胞。

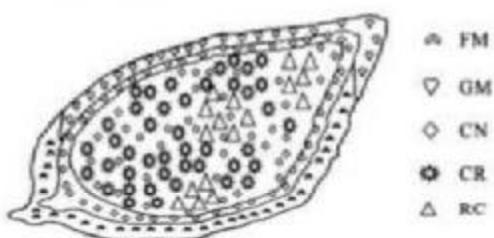


图1 中华乌塘鳢嗅上皮细胞分区示意图  
CN:纤毛非感觉细胞; CR:纤毛感受细胞; FM:指纹状嵴;  
GM:块状嵴; RC:柱状细胞

Fig. 1 Distribution patterns of an olfactory lamella of *Bestrichthys sinensis* Lacepede

CN:Ciliated non-sensory cell; CR:Ciliated receptor cell; FM:Fingerprint-like-pattern microridge; GM:Granule microridge; RC:Rod cell.

**2.2.1 纤毛非感觉细胞(ciliated non-sensory cell,简称CN)** 光镜下纤毛非感觉细胞呈椭圆形,单层,排列紧密平整。细胞质淡染,细胞核大,卵圆形(图版I-4)。扫描电镜下,纤毛非感觉细胞广泛分布于纤毛非感觉区和纤毛感觉区,并在上皮表面伸

出8~16根细长纤毛,长4.7~8.9 μm,直径0.19~0.27 μm,明显长于感受细胞的纤毛,纤毛弯向同一方向,呈波浪起伏状(图版II-1)。透射电镜下,纤毛微管结构为9+2式样,细胞体不向基膜延伸,也不在上皮表面形成嗅结,细胞游离面比纤毛感受细胞宽,纤毛的基部有丰富的线粒体(图版II-2)。

**2.2.2 纤毛感受细胞(ciliated receptor cell,简称CR)** 纤毛感受细胞为多层分布,所占区域比纤毛非感觉细胞大。纤毛感受细胞是一种双极神经元,细胞呈细长梭形,细胞质嗜碱性,核长梭形,位于细胞中央(图版I-4)。纤毛感受细胞位于感觉区,树突延伸至上皮的游离面,前端有膨大的嗅结,呈扁圆型,有的较饱满(图版II-3),有的较扁平(图版II-4)。嗅结的外缘伸出1~11根纤毛,比非感觉纤毛粗短些,长0.2~4.6 μm,直径0.25~0.31 μm,嗅结及其纤毛呈向日葵状。每个嗅结伸出的纤毛数量不等,纤毛的发育程度也不同,有的嗅结具6~11根发育完整的纤毛;有的仅2~3根发育完整的纤毛,其余发育不完全;也有的甚至没有纤毛,只有一圈小突起,这些小突起是正在发育中的纤毛(图版II-4)。纤毛内微管排列也为9+2结构;轴突延伸穿过基层,于固有层汇合成嗅神经纤维,与嗅叶相连。纤毛感受细胞胞质电子密度致密,其内有纵向平行排列的粗面内质网,大量线粒体分布于细胞的上半部(图版II-5)。

**2.2.3 柱状细胞(rod cell,简称RC)** 分布于感觉区,与纤毛感受细胞、纤毛非感觉细胞和支持细胞混杂在一起,呈区域性分布。柱状细胞在游离面呈圆锥状突起,基部较宽,直径0.8~1.7 μm,柱长3.5~7.2 μm(图版II-6)。圆锥状突起内有多根从其基部发出的成束微管。每个柱状细胞的横切面可见多个9+2微管结构。在圆锥状突起及其基部充满小泡,小泡内分布着许多线粒体(图版II-7)。

**2.2.4 支持细胞(supporting cell,简称SC)** 位于中下层,细胞呈长梭形,强嗜碱性(图版I-4)。支持细胞位于感觉区,表面有较粗短的小指状突起(图版II-3)。支持细胞紧密排列于纤毛感受细胞的两侧,细胞贯穿于整个嗅上皮层,细胞质电子密度稀疏,细胞内有较多的小泡和高尔基体,还有少量的线粒体、内质网和核糖体(图版II-8)。细胞的下部向感受细胞伸出小足,相邻两支持细胞之间通过小足形成镶嵌连接(图版II-9)。

**2.2.5 基细胞(basal cell,简称BC)** 位于最底

层,分布于基膜处(图版 I - 4),细胞体积小,形状不规则,细胞核占细胞的大部分,电子密度致密,有的基细胞孕育着子细胞(图版 II - 10)。

### 3 讨论

中华乌塘鳢是一种海洋洞穴硬骨鱼类,为防止泥沙阻塞鼻孔,中华乌塘鳢在漫长的适应过程中形成了封闭式嗅囊,只由前、后鼻孔与外界相通,嗅囊位于鼻腔深层,前鼻孔为狭小的管状开口,外部包被皮肤,可防止泥沙侵入。中华乌塘鳢前鼻腔内壁由上皮细胞构成,上皮细胞之间分散着许多杯状细胞,起分泌黏液的作用。

Yamamoto 等<sup>[4]</sup>研究了日本海 18 个月 100 多种真骨鱼类嗅上皮的显微和亚显微结构,根据感觉上皮和非感觉上皮在嗅板表面的 4 种分布情况,将嗅板表面感觉上皮划分为 4 种类型(图 2):I 型(感

觉区连续分布)、II 型(感觉区断续分布)、III 型(感觉区网状分布)、IV 型(感觉区斑状分布)。主要依靠嗅觉进行摄食等活动的鱼类,即嗅觉鱼类属于 I 型或 II 型,如鲑科(Salmonidae)、鳗鲡科(Anguillidae)、鲇科(Siluridae)、鳕科(Gadidae)<sup>[4]</sup> 和牙鲆(*Paralichthys olivaceus*)<sup>[5]</sup> 等;而主要依赖视觉进行活动的鱼类,即视觉鱼类则属于 III 型或 IV 型,如鲱科(Hemirhamphidae)、刺鱼科(Gasterosteidae)、鲹科(Carangidae)、鲀科(Tetraodontidae)、鱥科(Cyprinodontidae)、银汉鱼科(Atherinidae)<sup>[4]</sup> 和黑鲷(*Sparus macrocephalus*)<sup>[6]</sup> 等。中华乌塘鳢感觉上皮和非感觉上皮的分布属于 I 型,外侧为非感觉区,内侧为连续分布感觉区,因此作者认为中华乌塘鳢属于嗅觉鱼类,这与该种类栖息于光线较弱的深水洞穴、视觉较弱相适应。

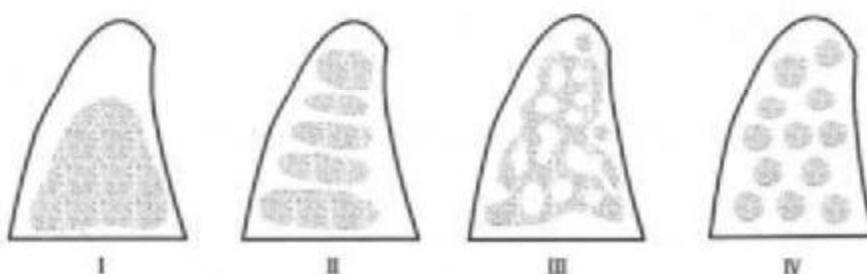


图 2 嗅板表面感觉上皮的 4 种分布类型<sup>[4]</sup>

I : 连续分布型; II : 断续分布型; III : 网状分布型; IV : 斑状分布型

Fig. 2 Four types of distribution patterns of the sensory epithelium

(shown by dotted areas) on the lamellar surface<sup>[4]</sup>

I : Continuous distribution; II : Uncontinuous distribution; III : Netlike distribution; IV : Dotted distribution

嗅囊是水动力器官,有 3 种方式使水从前鼻孔进入鼻腔,再从后鼻孔流出<sup>[7~9]</sup>:第 1 种是纤毛摆动型,属于这一类型的鱼类(如鳗鲡)具有许多纤毛非感觉细胞,纤毛的同步摆动起了蠕动泵的作用,使水流连续地流过嗅囊;第 2 种是副嗅囊活动型,这一类鱼类(如鲤鱼和鲇鱼)的嗅囊与 1~2 个副嗅囊相连,副嗅囊起泵的作用,靠近前鼻孔的嗅上皮较平坦,后鼻孔有一个具阀门作用的瓣膜,由于呼吸运动和口腔的启闭,使副嗅囊的体积扩大或缩小,将水从前鼻孔吸入,后鼻孔泵出,形成间歇的水流通过嗅囊;第 3 种是中间型,这一类型的鱼类(如斑月鳢)同时具有纤毛和副嗅囊,两者共同作用使水流通过嗅囊。中华乌塘鳢没有副嗅囊,但有大量的非感觉细

胞的纤毛,应属于第 1 种类型。这与中华乌塘鳢的穴居生活相适应,它不需要频繁的呼吸运动或口腔的启闭,只靠纤毛的摆动就可以推动水流不断地通过嗅囊,使嗅上皮及时感受水中各种物质的刺激。

为了探讨嗅觉器官结构与功能的关系,作者采用 EOG 记录方法,在非感觉区和感觉区记录了中华乌塘鳢对 DL-甲硫氨酸(DL-Met)的嗅觉电反应<sup>[10]</sup>,结果表明,在非感觉区几乎记录不到 EOG;在感觉区的不同部位可记录到大小不同的 EOG。作者认为这是因为在非感觉区只有表皮细胞和纤毛非感觉细胞,它们不存在气味物质的受体(odor receptor),故不能感受刺激物也就不产生 EOG;而在感觉区的不同区域,由于纤毛感受细胞、柱状细胞和

纤毛非感觉细胞分布不均匀,如在纤毛感受细胞密集区,可记录到大的EOG,而在纤毛非感觉细胞密集区,则只能记录到很小的EOG,这说明在感受细胞密集的区域,EOG反应最大。

在中华乌塘鳢的嗅觉电生理实验中,发现了中华乌塘鳢嗅上皮对性外激素的敏感性与性成熟度明显相关,对于同一种性外激素的刺激,性成熟个体产生的EOG幅值明显大于性未成熟个体<sup>[3]</sup>。组织学观察表明,中华乌塘鳢的嗅上皮纤毛感受细胞的形态可随不同的发育阶段而发生变化,性成熟鱼的嗅上皮纤毛感受细胞的嗅结有扁平型和饱满型两种,而性未成熟鱼没有扁平型嗅结,提示扁平型嗅结的纤毛感受细胞可能是感受性外激素的细胞。

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## Morphology and structure of olfactory organ in *Bostrichthys sinensis*

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**Abstract:** Morphology and structure of olfactory organ were systematically investigated by means of histology and electron microscopy in Chinese black sleeper *Bostrichthys sinensis* Lacepede. The results were as follows: Chinese black sleeper has a pair of fusiform olfactory sacs in front of the eyes; each sac has an incurrent and an excurrent nostril. There are 10-16 primary olfactory lamellae radiating from the wall of olfactory chamber in the fish, longitudinally arranging and paralleling to each other. The primary olfactory lamellae are different in height, and the one situating at the central part of the olfactory chamber is the highest, reaching the other part of the chamber. The primary lamellae contain second lamellae in order to enlarge the olfactory epithelium area. The lamellae are composed of two layers of olfactory epithelium and a central core. The central core is located at the central part of olfactory lamellae, composed of collagenous fiber, reticular fiber and blood capillary. The olfactory epithelium consists of many layers of cells, with a layer of cilia in the free surface orienting in the same direction. Under scanning electron microscopy, the olfactory epithelium consists of sensory and non-sensory areas. Non-sensory region at the margin of the lamella is thinner and smoother. Under high amplification, non-sensory area is composed of fingerprint-like-pattern microridges and granule microridges. Some microholes with the vesicle secretion among these two microridges are observed. Sensory area is continuous in the center, composed of many kinds of cells, ciliated receptor cell, ciliated non-sensory cell, rod cell and supporting cell. No microvillous receptor cells are observed. Ciliated non-sensory cells are widely distributed in non-sensory area and sensory area, each protruding 8-16

thin and long cilia, which are 4.7–8.9 μm long and 0.9–0.27 μm wide. Ciliated receptor cells are distributed in sensory area, each having an olfactory knob, from which 1–11 cilia protrude, and the cilia are 0.2–4.6 μm long and its diameter is 0.25–0.31 μm, which are shorter and wider than the cilia of ciliated non-sensory cell. Mature *Bostrichthys sinensis* Lacepede has two types of olfactory knob: full and flat, while immature one just has the full type olfactory knob. It suggested that the ciliated receptor cells with flat knob be sex pheromones' receptors while those with full knob are amine acids' receptors. Rod cells are distributed in sensory area and are often mixed with other types of cells. It has a rod-shaped protrusion, which is 3.5–7.2 μm long and 0.8–1.7 μm wide. Supporting cells are generally distributed in the sensory area with micro-protrusions. Under transmission electron microscopy, the olfactory epithelium is mainly composed of ciliated receptor cells, ciliated non-sensory cells, supporting cells, rod cells and basal cells. According to the location of cell nucleus, ciliated non-sensory cells are on free surface, and ciliated receptor cells and rod cells are next to ciliated non-sensory cells, followed by supporting cells and the basal cells at the bottom. The cilia of ciliated receptor cell and ciliated non-sensory cell both have 9+2 microtubule structure. The olfactory receptor cell is a bipolar neuron, protruding a single dendrite to the surface and a thin axon to the opposite direction. The axons pass through the basal lamina of epithelium, aggregating to form larger bundles, which connect to the olfactory lobe. The terminal of dendrite swells to form the olfactory knob, which slightly protrudes from the epithelial surface. There are bundles of microtubules in rod cell's protrusion and many mitochondria in rod cell; the microtubules also have 9+2 structure. The support cells lie tightly beside the ciliated receptor cell. The support cell stretches a little foot from its bottom and the two adjacent little feet would form the interdigititation. The basal cell's nucleus is large and occupies the most of the whole cell and some of the basal cells have sub-cells.

**Key words:** *Bostrichthys sinensis* Lacepede; olfactory organ; morphology and structure

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### 图版 I 说明

- 1: 中华乌塘鳢前鼻孔(IN)、后鼻孔(EN)、嗅囊(OS)的位置和外形, 左下: 嗅囊未剪开时的外形; 右下: 嗅囊剪开后的外形。 $\times 10$ .
- 2: 中华乌塘鳢嗅囊横切面, 示初级嗅板(POL)、次级嗅板(SOL)、嗅上皮(OE)和中央髓(CC).  $\times 40$ .
- 3: 光镜下中华乌塘鳢的单个嗅板横切面, 示嗅上皮(OE)和中央髓(CC).  $\times 100$ .
- 4: 中华乌塘鳢的嗅上皮(OE), 示细胞分层: 纤毛非感觉细胞(CN)、纤毛感受细胞(CR)、支持细胞(SC)、基细胞(BC).  $\times 1000$ .
- 5: 扫描电镜下中华乌塘鳢的单个嗅板(OL).  $\times 37$ .
- 6: 中华乌塘鳢非感觉区的指纹状嵴(FM), 示小孔(PO)及分泌物(VS).  $\times 15000$ .
- 7: 中华乌塘鳢非感觉区的块状嵴(GM), 示分泌物(VS).  $\times 750$ .
- 8: 中华乌塘鳢的纤毛非感觉区.  $\times 3000$ .

### 图版 II 说明

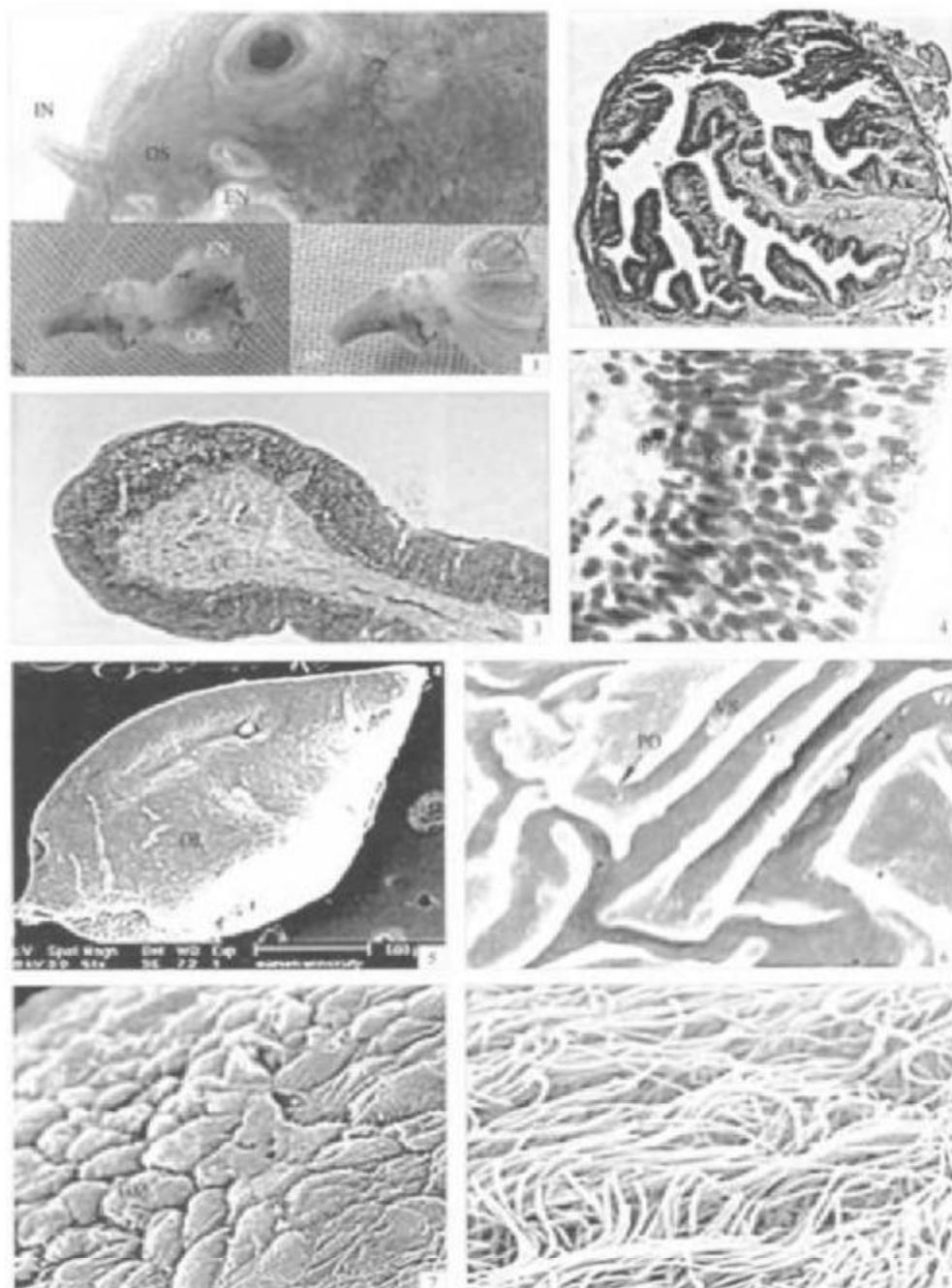
- 1: 扫描电镜下中华乌塘鳢感觉区的纤毛非感觉细胞(CN).  $\times 3600$ .
- 2: 透射电镜下中华乌塘鳢感觉区的纤毛非感觉细胞(CN), 左: 纤毛(Ci),  $\times 27000$ ; 左上: 9+2 结构,  $\times 40000$ ; 右: 线粒体(Mi),  $\times 10000$ .
- 3: 扫描电镜下中华乌塘鳢感觉区的纤毛感受细胞 CR(饱满型)和支持细胞(SC), 示嗅结(OK).  $\times 11000$ .
- 4: 扫描电镜下中华乌塘鳢感觉区的纤毛感受细胞 CR(扁平型), 示嗅结(OK)、嗅结上的小突起(P)及发育中的纤毛(DC).  $\times 3000$ .
- 5: 透射电镜下中华乌塘鳢感觉区的纤毛感受细胞(CR), 左: 细胞核(N), 树突(De), 轴突(Ax).  $\times 8000$ ; 右上: 嗅结(OK)横切面,  $\times 20000$ ; 右下: 嗅神经(ONF)横切面,  $\times 27000$ .
- 6: 扫描电镜下中华乌塘鳢感觉区的柱状细胞(RC).  $\times 3600$ .
- 7: 透射电镜下中华乌塘鳢感觉区的柱状细胞(RC), 示微管(Mt)及线粒体(Mi).  $\times 27000$ .
- 8: 透射电镜下中华乌塘鳢感觉区的支持细胞(SC).  $\times 20000$ .
- 9: 透射电镜下中华乌塘鳢感觉区的支持细胞(SC), 示镶嵌连接(Id).  $\times 20000$ .
- 10: 透射电镜下中华乌塘鳢感觉区的基底细胞(BC).  $\times 6700$ .

### Explanation of Plate I

- 1: The location and shape of incurrent nostril (IN), excurrent nostril (EN) and olfactory sac (OS) of *Bostichthys sinensis*. Down left: the shape of olfactory sac (close). Down right: the shape of olfactory sac (open).  $\times 10$ .
- 2: Transverse section through the olfactory sac of *Bostichthys sinensis*, indicating primary olfactory lamella (POL), secondary olfactory lamella (SOL), olfactory epithelium (OE) and central core (CC).  $\times 40$ .
- 3: Transverse section through the olfactory lamella of *Bostichthys sinensis*, indicating olfactory epithelium (OE) and central core (CC).  $\times 100$ .
- 4: The olfactory epithelium (OE) of *Bostichthys sinensis*, indicating the layers of cells: ciliated non-sensory cell (CN), ciliated receptor cell (CR), supporting cell (SC) and basal cell (BC).  $\times 1000$ .
- 5: The shape of single olfactory lamella (OL) by SEM.  $\times 37$ .
- 6: The fingerprint-like microridge(FM) in non-sensory area of olfactory epithelium, indicating the pore(Po) and vesicle secretion(VS).  $\times 15000$ .
- 7: The granule microridge(GM) in non-sensory area of olfactory epithelium, indicating vesicle secretion(VS).  $\times 750$ .
- 8: The ciliated non-sensory area of olfactory epithelium.  $\times 3000$ .

### Explanation of Plate II

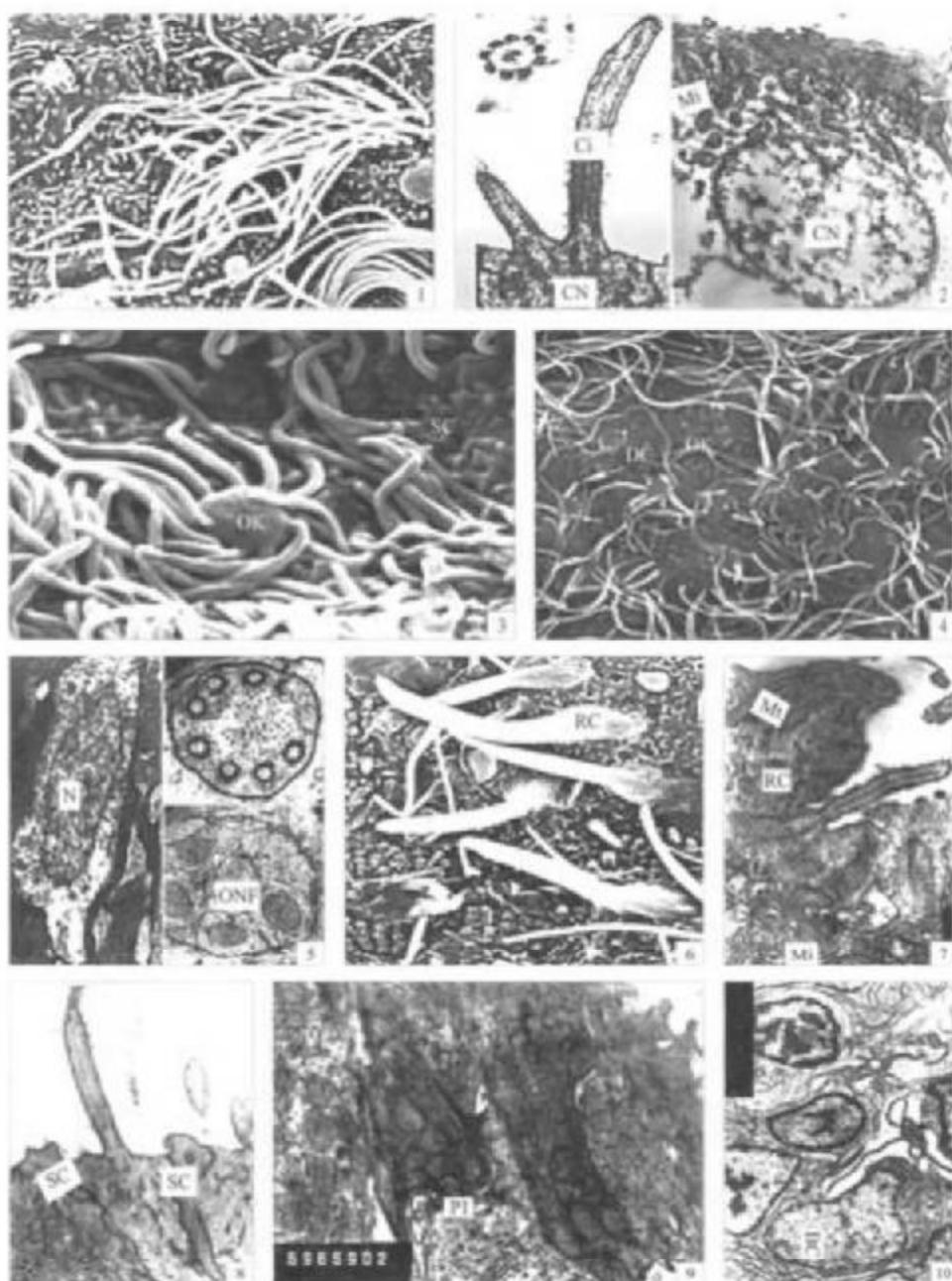
- 1: The ciliated non-sensory cell (CN) in the sensory area by SEM.  $\times 3600$ .
- 2: The ciliated non-sensory cell (CN) in the sensory area by TEM. Left: cilia (Ci),  $\times 27000$ . Left up: 9+2,  $\times 40000$ . Right: mitochondria (Mi),  $\times 10000$ .
- 3: The ciliated receptor cell (CR) (full type) and support cell (SC) in the sensory area by SEM, indicating olfactory knob (OK).  $\times 11000$ .
- 4: The ciliated receptor cell (CR) (flat type) in the sensory area by SEM, indicating olfactory knob (OK), the protrusions (P) from OK and developing cilia (DC).  $\times 3000$ .
- 5: The ciliated receptor cell (CR) in the sensory area by TEM. Left: nucleus (N), dendrite (De), axon (Ax),  $\times 8000$ . Right up: the Transverse section of OK,  $\times 20000$ . Right down: the Transverse section of olfactory nerve fiber (ONF),  $\times 8000$ .
- 6: The rod cell (RC) in the sensory area by SEM.  $\times 3600$ .
- 7: The rod cell (RC) in the sensory area by TEM, indicating microtubule (Mt) and mitochondria (Mi).  $\times 27000$ .
- 8: The support cell (SC) in the sensory area by TEM, indicating the interdigitation(Id).  $\times 20000$ .
- 9: The support cell (SC) in the sensory area by TEM, indicating the interdigitation(Id).  $\times 20000$ .
- 10: The basal cell (BC) in the sensory area by TEM.  $\times 6700$ .



图版 I Plate I  
(图版 I 说明见第 530 页 Explanation of Plate I at page 530)

马细兰等:中华鸟塘鳢嗅觉器官的形态结构

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图版 II Plate II  
(图版 II 说明见第 530 页 Explanation of Plate II at page 530)