

两栖动物性二型的研究进展

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摘要: 两栖动物性二型(sexual dimorphism)是指同种雌雄个体间在形态、行为及生理功能等方面表现出的稳定差异,是动物行为学、神经生物学、进化生物学和生态学研究的重要内容。作为自然选择与性选择共同作用的产物,性二型直接关乎个体的生存与繁殖,并深刻影响种群演化。近年来,随着分子生物学和多组学技术的发展,性二型的形成机制得到了更为深入的阐释。本文综述了两栖动物性二型的主要类型、生态及进化意义,聚焦于环境因素对性二型可塑性的影响,并深入评述了其分子调控机制的最新进展。在此基础上,本文展望了未来的研究方向,以期在两栖动物多样性保护及相关生物学基础研究提供理论参考。

关键词: 性二型;自然选择;性选择;多组学

中图分类号: Q16; Q954 **文献标识码:** A

Advances in research regarding sexual dimorphism in amphibians

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Abstract: Sexual dimorphism (SD) in amphibians encompasses consistent differences in morphology, behavior, and physiological functions between sexes. As a fundamental topic in evolutionary biology and ecology, SD arises from the interplay of natural and sexual selection, and exerts profound effects on individual fitness, population dynamics, and evolutionary trajectories. Amphibians, with their dual aquatic-terrestrial life history and high environmental sensitivity, provide a valuable model for exploring the evolutionary drivers of SD and the role of phenotypic plasticity. Although patterns of amphibian SD have been extensively described, knowledge remains limited on how environmental factors influence trait plasticity and the molecular networks linking genotype to phenotype. Drawing upon morphological, ecological, and multi-omics evidence, this study systematically reviews the diversity of SD forms in amphibians, analyses its ecological and evolutionary drivers, and highlights recent advances in understanding environment-driven plasticity and molecular regulation under global climate change. Amphibian SD exhibits considerable diversity in form and function. Sexual size dimorphism (SSD) is the most widespread pattern, with approximately 90% of anuran species having females larger than males, generally driven by fecundity selection to maximize egg production. In contrast, species with strong male-male competition evolve larger males through sexual selection. Structural dimorphism often involves male-specific traits that enhance mating success, such as keratinized maxillary spines in *Leptobrachium leishanense* for combat. Morphological and physiological divergence can directly shape individual survival and reproductive strategies, as shown in *Xenopus laevis*, where males and females exhibit differential sensitivity to specific frequency ranges of the courtship calls. SD in amphibians is highly plastic in response to both climatic and non-climatic environmental change. Temperature and precipitation are major climatic drivers. In regions with high temperature seasonality, males may show proportionally greater size increase than females, whereas spatial or temporal variation in rainfall can alter breeding season length and sex-specific growth rates, as reported for *Lithobates sylvaticus*. Non-climatic pressures, including habitat fragmentation and island isolation, can alter SD patterns; island populations of *Odorrana schmackeri* show notable female dwarfism due to limited food resources, reducing SSD. Predation risk can constrain the development of sexual traits or favor defensive adaptations, such as enlarged toxin glands in *Epidalea*

收稿日期: 2025-06-11; 修回日期: 2025-08-02

基金项目: 国家自然科学基金项目(32170429); 四川省科技计划项目 (2025NSFSC2131); 西华师范大学基础科研业务费(23kq005)

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calamita or altered coloration strategies. Recent advances in molecular biology and multi-omics approaches have enabled deeper insights into the underlying mechanisms driving SD. Sex-determining genes such as *dm-w* and *dmrt1* in *Xenopus* trigger cascades of sex differentiation during embryonic development. Sex hormones regulate the development of external traits and influence neurosteroid pathways, thereby shaping courtship call production and auditory sensitivity thresholds in *Hyla cinerea*. Integrated transcriptomic and metabolomic data show that male-specific morphological traits are maintained through particular metabolic pathways. In *Bufo gargarizans*, the development of robust forelimb muscles for amplexus is associated with activation of energy metabolism and protein synthesis pathways involving genes such as *AGXT* and *ACADL*. In *L. leishanense*, spine formation is linked to Wnt signaling pathway activity and expansion of keratin gene families. In summary, amphibian SD arises from the integrated effects of genetic architecture, endocrine regulation, and environmental forces. While research has progressed from phenotypic description to mechanistic inquiry, significant knowledge gaps persist. These include the neural basis of sexually dimorphic behaviors, the contribution of epigenetic mechanisms to rapid adaptation and transgenerational effects, and the utility of SD traits as bioindicators in conservation. Addressing these questions will advance our understanding of SD evolution and inform effective conservation strategies in the face of ongoing environmental change.

Key words: sexual dimorphism; natural selection; sexual selection; multi-omics

两栖动物(amphibians)作为脊椎动物中从水生到陆生转变的重要类群,主要分为三个目:蛙类(无尾目)、蝾螈(有尾目)和蚓螈(无足目),广泛分布于全球各地,尤其在湿地、热带雨林等生态环境中^[1]。两栖动物对环境变化高度敏感,因此被视为重要的生态指示物种^[2,3]。近年来,随着生物多样性保护研究的深入,两栖动物的行为、生理和生态特征受到了越来越多的关注,其中,性二型(sexual dimorphism)作为一种显著的生物学现象,受到越来越多的关注。

性二型是指性成熟的雌雄个体在形态、行为及生理功能等方面表现出的差异,这种现象在无脊椎动物和脊椎动物中都广泛存在^[4,5]。在两栖动物中,性二型主要体现在体型、体重、体色、行为、发声结构等多个方面^[6,7]。例如某些蛙类,雄性通常比雌性体型更小,但声囊更为发达,以增强繁殖季节吸引雌性的求偶能力^[8]。性二型特征的演化和表现与繁殖成功率、性别角色分工等行为特征密切相关,进而影响个体的生态适应性^[9-11]。因此,研究两栖动物的性二型及其潜在机制,有助于揭示不同性别在环境变化中所采用的不同适应策略,这对全球气候变化和栖息地破碎化加剧背景下濒危物种的保护具有重要参考价值。

尽管目前关于两栖动物性二型的研究取得了显著进展,但仍存在诸多亟待解决的科学问题。首先,不同性别间形态结构和生理功能差异的生态学和进化意义尚未得到充分阐释;其次,环境因素(如气候变化及栖息地破碎等)对性二型表现的影响机制仍不明确,特别是在全球气候变化背景下,这一问题显得尤为重要;此外,分子水平上的性二型机制研究相对滞后,如性别决定基因、性激素调控网络等方面

的知识仍有待完善。本文旨在系统梳理两栖动物性二型研究的最新进展,阐述其生态意义和演化机制,并就当前研究现状进行深入分析,以期对相关保护策略的制定提供理论依据。

1 两栖动物性二型的类型

1.1 体型性二型

体型性二型是指雌雄成熟个体间在体长或体重上存在显著差异,这一现象在两栖动物中普遍存在(图1A)。一项针对589种蛙类的研究表明,90%的物种中雌性个体显著大于雄性,3%的物种雄性个体大于雌性,而7%的物种则未表现出明显的体型性二型现象^[12]。雌性体型较大通常与其较高的繁殖投入密切相关,体型较大的雌性能够产下更多或体积更大的卵,进而提高繁殖成功率。相反,在某些物种中,体型较大的雄性在雄雄竞争中更具优势,体型差异有助于其在争夺配偶的过程中获得更多的机会^[13]。类似的体型性二型现象也广泛存在于大多数蝾螈和蚓螈物种中,这些物种的雌性个体同样显著大于雄性^[14]。

1.2 体色性二型

体色性二型是指在同一物种中,雄性和雌性个体在皮肤颜色上表现出显著差异,包括颜色的深浅、图案的复杂程度以及色彩的多样性等方面(图1B)^[15]。根据体色变化的方式和发生时期,体色性二型主要分为两类:动态体色性二型(dynamic dichromatism)和个体发生体色性二型(ontogenetic dichromatism)^[16]。动态体色性二型通常出现在雄性个体中,是一种在繁殖期间出现的暂时性体色变化,持续时间从数天到数周不等,其主要功能是吸引雌性进行交配,增强雄性的繁殖成功率^[17]。个体发生体色性二型则存在

于性成熟的雌性或雄性个体中,是一种伴随个体发育而产生的长期体色变化。例如,金斑囊蛙(*Gastrotheca aureomaculata*)幼体通体呈绿色,至成体阶段雄性转变为棕褐色而雌性维持绿色,形成显著的体色性二型模式,这种分化可能受到配偶选择与捕食压力的共同驱动^[18]。

1.3 结构性二型

结构性二型指的是两性个体在特定器官或身体结构上呈现出的性别差异,这些差异通常体现在形态、结构或尺寸等方面,并且与个体生态适应性密切相关(图1C)。一方面,为应对激烈的雄性竞争并提高繁殖成功率,一些两栖动物雄性演化出特殊的结构性特征。例如,雷山髭蟾(*Leptobrachium leishanense*)作为我国特有的两栖物种,雄性在繁殖期上颌部位会长出坚硬的黑色角质刺。雄性通过角质刺与其他同种雄性进行“角斗”,以此竞争配偶。该角质刺在繁殖季节发挥重要作用,但在繁殖期过后会自然脱落^[19]。另一方面,与两栖动物声音通讯密切相关的器官也表现出显著的结构性二型。以非洲爪蟾(*Xenopus laevis*)的发声器官为例,成年雄性喉部肌肉纤维数量可达雌性的八倍,且均为支持快速鸣叫的快肌纤维,有助于产生快速、复杂的求偶叫声^[20]。在南美泡蟾(*Physalaemus pustulosus*)中,研究发现两性幼体时期喉部结构相似,然而随性成熟进程,成年雄性喉部的体积、声带及纤维结构均表现出显著的正向异速生长,而雌性喉部则变化较小,从而为雄性复杂的鸣声行为奠定了形态学基础^[8]。此外,在听觉器官上,雄性牛蛙(*Rana catesbeiana*)的鼓膜面积约为雌性的两倍,其上附着的软骨垫也更重。这种结构上的差异导致雌雄个体在听觉感知上出现差异,雄性在低频区听觉更敏感,而雌性则在高频区表现更佳,反映了响应不同声音信号或同一声音中不同频率成分的性别适应性分化^[21]。

1.4 行为与生理的性二型

行为与生理的性二型是指在物种的行为模式、感官感知以及生理功能上的两性差异,是结构性二型在功能层面的体现,共同决定了个体的生存和繁殖策略。其中,信号通讯行为及其感知尤为显著。在许多两栖类物种中,雄性通过鸣声吸引雌性并进行领地宣示,而雌性则依据鸣声的一系列声学特征(如频率、强度、时长等)进行配偶选择(图1D)。以南美泡蟾(*P. pustulosus*)为例,研究发现雄性在

whine音节后面添加多个chuck音节形成组合鸣叫,同时配合喉囊的节律性膨胀作为视觉信号,能显著增强对雌性的吸引力^[22]。此外,部分物种的雌性也能主动发出求偶鸣声。例如,雌性凹耳溪蛙(*Odorrana tormota*)发声时间较短,鸣叫中非线性现象较少,声学结构相对简单,与雄性的发声特征形成明显对比^[23]。非洲爪蟾(*X. laevis*)的雌性可以发出两种不同类型的鸣叫:一种是节奏较慢的节拍式鸣叫(ticking),主要用于拒绝雄性的求偶行为;另一种是节奏较快的敲击式鸣叫(rapping),出现在排卵前的短暂发情期,能够有效激发雄性接近并发出应答鸣叫,雄性则会改变其鸣声的结构作为回应,最终形成协调的二重唱以增强繁殖成功率^[24]。这种发声上的性别差异可能归因于两性间喉部肌肉生理兴奋性和肌电增强效应的差异^[25,26]。与之相对应,声音信号的感知同样存在显著的性别分化。例如,在非洲爪蟾(*X. laevis*)的外周听觉系统中,雌性表现出对雄性求偶鸣叫中关键频率的特化敏感性,而雄性则对同性竞争相关的信号频率更为敏感。这种性别特异性的听觉调控过程高度依赖于内分泌系统,具有明确的激素依赖性^[27]。在中枢神经系统中,两性的听觉感知呈现出复杂的脑半球不对称性:即雌性在处理种内通讯信号时表现出左半球优势,而雄性在应对潜在威胁信号时则呈现右半球优势。这一功能性偏侧化被认为与两性在繁殖和生存中所面临的不同生态选择压力紧密相关^[28]。除声音信号外,许多蛙类在繁殖季节存在对视觉信号感知的性别差异。例如,针对南美泡蟾(*P. pustulosus*)的电生理学研究

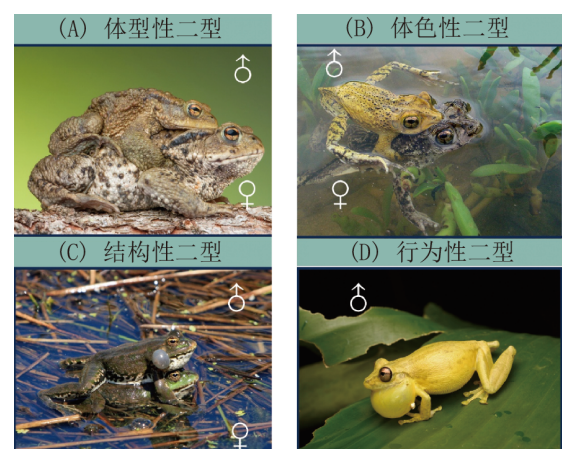


图1 两栖动物性二型的主要类型

Figure 1 Major types of sexual dimorphism in amphibians

发现,在激素诱导的繁殖状态下,雌性的视网膜在暗光条件下的光敏感度会显著提升,而雄性则无此变化,这使得雌性在进行夜间择偶时,具备了更强的视觉探测能力,能更有效地评估雄性的视觉求偶信号^[29]。除发声行为外,抱对行为是两栖类另一种典型的性二型行为表现。雄性个体为了在交配时牢固地抓住雌性以确保体外受精成功,其前肢肌肉通常更为发达,肌纤维直径更大、数量更多,蛋白质含量也更高^[30-32]。这些结构上的差异在生理功能层面则体现为更大的绝对力量、更长的收缩-舒张周期以及更强的抗疲劳能力^[33,34]。行为性二型的实现依赖于特定的生理基础,而生理的性二型又通过特定行为模式体现出来,二者相互协同,共同促进了两栖动物性二型特征的形成与进化。

2 两栖动物性二型的生态与进化意义

2.1 性二型的生态意义

2.1.1 性二型对栖息地利用及生态位分化的影响

两栖动物的性二型不仅表现为形态和生理特征的差异,还反映在资源利用、活动空间及行为策略上,进而影响性别间的栖息地选择和生态位分化^[35]。这种性别特异性策略能够有效减少性别间资源竞争,促进种群内生态稳态,进而影响生态系统的多样性和稳定性^[36]。例如,成年雌性的绿东美螈(*Notophthalmus viridescens*)头部一般明显大于雄性,这一形态差异伴随着不同的捕食习性:雄性个体以浮游动物为主要食物,而雌性个体偏好捕食水体底部的特定猎物种类^[37]。这种栖息地与食性方面的性别分化,有效降低了性别间竞争,并通过不同的捕食压力影响猎物群落结构,体现了性二型在生态系统多层面的功能。

2.1.2 性二型与反捕食等生态行为的关系

两栖动物的性二型性状也可以影响其反捕食策略,提升生存能力^[38]。例如,雄性绿背蟾蜍(*Epidalea calamita*)背部肤色较浅且色素更浓,这不仅可以作为吸引雌性的视觉信号,也可以作为警戒色,减少捕食风险^[39]。此外,两性间的运动差异也影响其生存策略,雄性通常运动速度更快,有助于追捕猎物及逃避捕食者^[40]。相较之下,雌性由于携带较重卵块,体型偏大,常通过增加腿长及肌肉量来补偿跳跃性能的下降^[41]。这种功能与形态的协同性二型,是两栖动物适应不同生态压力的体现。

2.1.3 个体生存率与繁殖成功率

性二型特征可以影响个体适应度,显著提升两栖动物的生存和繁殖成功率。例如,雄性蛙类通过诸如婚垫、发达的抱对肌、声囊以及鲜艳的体色等特殊结构来吸引雌性完成交配;同时,这些特征也用于雄性之间的竞争,以确保其繁殖优势^[30,42,43]。我们前期研究发现,雄性成年中华蟾蜍(*Bufo gargarizans*)的前肢桡侧腕屈肌较雌性明显发达,有助于雄性在繁殖期稳固环抱雌性,并降低雄性竞争者的干扰^[31]。雌性个体由于需要繁育大量后代,在生殖力选择压力下,个体体型往往较大,以容纳更多的卵子,从而提高其繁殖成功率^[44]。

2.2 性二型的进化意义

2.2.1 性选择

两栖动物性二型的形成是种群在性选择和自然选择等多重选择压力下适应环境的结果。性选择假说最早由达尔文在1871年的《人类的由来及性选择》中提出,该学说认为某些特征虽然对动物的生存没有直接益处,甚至可能会带来负面影响,但如果能够提升个体的交配成功率,两性间的这些差异特征将在进化过程中得到强化,从而导致性二型的产生^[45]。例如,雄性通常进化出夸张的性状(如鲜艳体色、复杂鸣叫等)以增强配偶吸引力和竞争优势,雌性则注重生存和繁殖投资^[15]。

2.2.2 自然选择

自然选择假说认为,生态资源的竞争可能对两性施加不同的选择压力,促使性二型的进化^[46]。在两栖动物的种群中,种内竞争可能驱使雄性和雌性在生态位空间上发生分化,实现性生态位的分离,从而减轻种内生态竞争的强度。这种歧化选择(disruptive selection)压力促使雄性和雌性发展出不同的体型或采用不同的资源利用方式,以减少直接竞争^[47,48]。例如,生境的开放程度或植被覆盖水平会影响光照条件,进而影响个体的颜色感知及其捕食压力,从而驱动两性的形态和行为差异^[49]。性选择和自然选择压力并非相互独立,而是可以协同或相互作用,共同塑造性二型的多样性。

3 环境因素与两栖动物性二型的关系

两栖动物的性二型表现出较强的可塑性,其形成与维持受到多种环境因素的影响^[50]。随着全球气候变化和人类活动日益加剧,环境因子对两栖动

物性二型的作用机制已成为研究的热点。综合最新研究,当前影响两栖动物性二型的主要环境因素包括气候因子和非气候环境胁迫等。

3.1 气候因子对两栖动物性二型的影响

多项研究表明,两栖动物的性二型对气候因子(如温度和降水等)表现出显著的性别差异性响应。例如,Goldberg等^[51]针对南美树蛙(*Scinax fuscovarius*)的研究揭示,在不同地理范围和降水梯度条件下,性二型在空间分布上表现出异质性,特别是在降水减少的阿根廷西部地区,雌性体型的增幅显著超过雄性,形成了雌性偏大的性二型趋势。Sheridan等^[52]基于木蛙(*Lithobates sylvaticus*)的研究进一步证实了气候因子对性二型的影响:1901至1960年间,气温上升和无霜期延长显著影响了木蛙的体型,雌性体型与降水量及其与无霜期的交互作用均呈显著正相关,而雄性体型主要与降水量呈正相关。一项针对全球3 500余种两栖动物的大尺度数据分析显示,温度季节性变化是影响无尾两栖类体型性二型变异的最强气候因子。研究发现,随着温度变化的季节性波动幅度增加,雄性体型相对雌性增幅更大,表现为雄性偏大的性二型趋向^[53]。这一宏观气候梯度对性状演化的影响,可能与繁殖窗口的压缩和资源竞争压力增强有关,从而选择出性成熟更早、生长更快的雄性。

3.2 非气候因素对两栖动物性二型的影响

除了气候条件之外,其他非气候环境压力也是影响两栖动物性二型的重要因素,包括栖息地破碎化、捕食压力、人类活动及食物资源等^[54]。栖息地破碎化和人类干扰不仅导致两栖动物适宜生境面积的减少,还降低了生态环境的同质性,限制了雌雄个体间资源的差异化利用,从而影响性二型性状的演化^[52]。例如,Wu等^[55]比较了千岛湖岛屿与大陆的花臭蛙(*Odorranas schmackeri*)种群后发现,千岛湖岛屿上的雌性体型和口裂宽均显著小于大陆雌性,出现“岛屿侏儒化”现象,而雄性则无明显变化;进一步的分析表明,雌性体型变化主要受食物资源丰富度驱动;与此同时,岛屿种群的雌雄食物组成趋于一致,性别间生态分工减弱,证实了非气候因素对性二型的影响。类似地,另一项关于绿背蟾蜍(*Epidalea calamita*)的研究发现,农业生态系统下个体因面临更强的捕食压力,无论雌雄均表现出更大的毒腺和更鲜明的体色,其中雄性的特化现象更为突出。这

种性别差异化的形态响应,有助于提高个体的化学防御能力和生存适应性^[56]。实际上,多种环境因子往往同时作用并相互影响,并可能产生协同或拮抗效应,作用于性二型性状,甚至影响性别比例和种群适应能力^[57,58]。因此,理解环境因素与两栖动物性二型的关系,需要综合考虑多种因子的联合作用及其性别层面的差异性。

4 两栖动物性二型形成分子机理的研究进展

4.1 性别决定与遗传基础

性别决定机制为两栖动物性二型的形成奠定了遗传基础,主要体现在关键基因与不同性别及发育阶段的时空表达调控。例如,非洲爪蟾(*X. laevis*)W染色体特有的*dm-w*基因已被证实为雌性性别决定过程中的关键因子^[59]。该基因在ZW型(雌性)个体的原始性腺中特异性高表达,通过调控性别分化核心基因*dmrt1*进而促进卵巢分化。*Dmrt1*虽在雌雄个体中均表达,但其生物学作用存在显著性别依赖性:在雌性中,通过上调卵巢分化相关基因*foxl2*与*cyp19*等的转录活性维持卵巢发育;在雄性中,则调控睾丸发生及雄性第二性征发育进程。在另一项研究中,Kuhl等^[60]鉴定出*bod11*为欧洲绿蟾蜍(*Bufo viridis*)的性别决定候选基因,其在不同性别及发育阶段表现出明显分化表达。此外,雄性的Y染色体特异性非编码RNA(Y-specific non-coding RNA, ncRNA-Y)特异表达,表明转录后调控也参与性别决定过程。在功能基因层面,雄性个体中*sox9*、*sox10*与*sfl*等基因呈高表达,雌性则以*foxl2*、*wnt4*、*ihh*、*ptch1*、*gli3*和*fshr*为主,其中,*gdf9*、*cyp19*和*cyp17a1*等基因的表达仅在雌性晚期发育阶段检测到。综上所述,两栖动物的性别决定建立在多基因复杂调控网络之上,其功能和调控网络在不同物种、不同发育阶段及性别间存在显著差异。

4.2 激素信号与性二型塑造

两栖动物的性二型性状不仅受到性别决定基因的影响,还高度依赖于性激素及其受体的调控。研究表明,绿蛙(*Pelophylax esculentus*)脑组织内神经类固醇合成酶及性激素受体相关基因的表达存在明显的季节性和性别差异,提示脑内类固醇合成通路直接参与了性二型表型的季节性塑造^[61]。体色作为两栖动物重要的性二型特征,其动态变化同样依赖激素调控。以壮溪树蛙(*Buergeria robusta*)为例,

繁殖期雄性的体色转变为明亮的黄色以吸引配偶。实验证明,睾酮能促进雄性体表黄色素细胞分散,并与其他激素协同作用,通过抑制促黑素细胞刺激素合成等途径,直接促进黄色体色的形成^[62]。除视觉信号外,激素也参与对发声和听觉等行为的调控。雄蛙的鸣叫行为普遍依赖于雄激素和精氨酸加压催产素的激活^[63]。对应地,雌蛙对雄性求偶声的响应行为强度与体内雌激素水平密切相关。例如,雌性绿树蛙(*Hyla cinerea*)的听觉阈值在自然状态下显著低于雄性,但经睾酮处理后,其听觉阈值会升高至雄性水平,原有的性别差异随之消失^[64,65]。对南美泡蟾(*P. pustulosus*)的研究显示,仅当促性腺激素水平升高的雌性接收到雄性求偶信号时,其听觉中枢内作为神经激活分子标记的*egr-1*基因表达量才会协同性地显著增长^[66]。这些研究表明,激素及其相关信号通路不仅调控着体色等外部形态的分化,更精细地调节着声音通讯这类复杂行为中信号的产生与感知,为适应繁殖行为和环境选择压力提供了分子基础。

4.3 性二型性状的多层次调控网络

性别决定基因和激素信号启动了性别分化的级联反应,但具体性二型性状的形成则依赖于下游复杂的分子调控网络。近年来,多组学(Multi-omics)技术的发展为研究性二型的调控分子网络提供了全新的研究视角。通过整合基因组学、转录组学、蛋白质组学和代谢组学等多层次数据,可以更加系统和深入地解析性别特异性状的形成与调控过程^[67-69]。我们近期的研究发现,桡侧腕屈肌对于中华蟾蜍(*B. gargarizans*)雄性个体的抱对行为至关重要,雄性体内该肌肉的量显著高于雌性。通过对雄、雌样本的桡侧腕屈肌开展转录组和代谢组分析,我们发现差异表达基因主要富集在肌肉收缩、代谢、能量产生等生理过程,差异表达代谢物富集在蛋白质合成、氨基酸代谢与脂肪酸合成等通路。进一步联合分析显示,*AGXT*、*ACADL*、*ACAT1*、*MDH2*和*SUCLG2*等基因在相关代谢通路中发挥关键调控作用,提示这些基因及其代谢调控机制与桡侧腕屈肌的性二型密切相关^[70]。Li等^[71]以我国特有种雷山髭蟾(*L. leishanense*)为研究对象,通过高质量基因组组装及比较基因组分析,揭示了角蛋白基因家族的扩张及其在雄性角质刺等特殊结构中的高表达,为性二型结构遗传基础的解析提供了直接证据。进一步的转录组研究表明,角质刺的发生发育与Wnt信号通

路、雄激素合成及上皮分化等多条信号通路紧密相关,涉及一系列关键功能基因的协同调节,从而阐明了性激素信号、结构蛋白调控及组织分化等机制在雄性特化性状形成中的共同作用。凹耳臭蛙(*O. tormota*)为适应溪流环境的噪声影响,雄性进化出了超声波通讯能力,而雌性则不具备此能力,构成了一种典型的感知功能性二型。Chen等^[72]通过比较雌雄脑组织的转录组,发现雄性中上调的差异基因显著富集于神经发生、离子转运、信号转导以及能量代谢等与高频听力直接相关的生物学过程,从分子层面阐明了这一复杂感觉和行为性状的调控基础。综上所述,整合多层次调控信息的研究方法,通过解析从遗传变异、基因表达调控、信号通路激活到代谢重塑等不同层面的相互作用,能够系统性地构建并验证复杂的性二型调控分子网络,为全面理解这一重要进化适应现象的分子机制奠定坚实基础。

5 结论与展望

两栖动物性二型不仅是进化生物学的重要研究对象,也是保护生物学领域的关键问题之一。本文系统综述了两栖动物性二型的类型、其进化与生态意义、环境因素的影响,以及分子机制的最新研究进展。尽管近年来取得了一定进展,关于性二型形成机制的研究仍存在若干亟待解决的问题。首先,当前研究多集中于描述行为差异或其外周的形态生理基础,而对于调控这些性二型行为背后的神经机制仍知之甚少;其次,表观遗传和转录后调控层面的研究相对不足,对于性状可塑性及其功能多样性的分子基础了解尚不充分;此外,针对不同物种、不同地理种群及多样化生态环境下的系统性性二型比较和长期追踪研究仍显不足。因此,未来应加强神经行为学与功能基因组学等技术的融合,通过解析基因调控网络、神经环路及行为表型之间的关联,阐明性二型的神经生物学基础;同时,深化表观基因组等多组学整合分析,构建跨层次的分子调控网络,以揭示性状可塑性的深层调控机理;拓展结合长期野外监测与实验室控制实验的系统性比较研究,评估性二型在全球变化背景下的适应性潜力与脆弱性。这些研究的推进,将有助于全面揭示两栖动物性二型的发生机制和生态适应过程,为生物多样性的保护与管理提供更加坚实的科学支撑。

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