DESCRIPTIVE ANATOMY OF *EPIPLATYS SEXFASCIATUS* (CYPRINODONTIFORMES: APLOCHEILIDAE) AND A PHYLOGENETIC ANALYSIS OF EPIPLATINA

by

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ABSTRACT. - The external anatomy and osteology of *Epiplatys sexfasciatus* is described. The distribution of twelve characters of fin placement, the jaws, and hyobranchial apparatus, across ten species of Epiplatina, and an outgroup, is described. Four further characters defined the monotypic genera *Aphyoplatys* and *Pseudepiplatys*. Phylogenetic analysis using PAUP software was largely uninformative, while an UPGMA analysis proposed the hierarchy of relationships to be (*Aphyoplatys*, *Pseudepiplatys*), ((Callopanchina), ((*Epiplatys sexfasciatus*, *E. singa*, ((*E. sangmelinensis*, *E. spilargyreius*), (*E. bifasciatus*, *E. dageti*, *E. fasciolatus*, *E. multifasciatus*)))). The possible influence of paedomorphism on these analyses is discussed.

RÉSUMÉ. - Anatomie descriptive d'*Epiplatys sexfasciatus* (Cyprinodontiformes: Aplocheilidae) et analyse phylogénétique des Epiplatina.

L'anatomie et l'ostéologie d'*Epiplatys sexfasciatus* sont décrites ainsi que la répartition de douze caractères chez dix espèces d'Epiplatina et un groupe extérieur : position des nageoires, de la mâchoire et de l'appareil branchial. Les genres monotypiques *Aphyoplatys* et *Pseudepiplatys* sont définis par quatre caractères supplémentaires. L'analyse phylogénétique à l'aide de PAUP a apporté peu d'information tandis que l'analyse par UPGMA a proposé la hiérarchie de parenté suivante : (*Aphyoplatys*, *Pseudepiplatys*), ((Callopanchina), ((*Epiplatys sexfasciatus*, *E. singa*, ((*E. sangmelinensis*, *E. spilargyreius*), (*E. bifasciatus*, *E. dageti*, *E. fasciolatus*, *E. multifasciatus*)))). L'influence possible de la paedomorphose dans ces analyses est discutée.

Key words. - Cyprinodontiformes - Aplocheilidae - *Epiplatys* - Osteology - Paedomorphism - Phylogenetic analysis.

Epiplatys Gill, 1862 comprises approximately 50 species (Huber, 2000) of west and central Africa (Scheel, 1968). Two monotypic genera, *Aphyoplatys* Clausen, 1967 (from Congo), and *Pseudepiplatys* Clausen, 1967 (from Liberia), are thought to be closely related to *Epiplatys*. On the basis of evidence from meristics, karyotypy, cranial scale patterns, male ctenoidy, egg morphology, pigmentation, haemoglobin electrophoresis, and experimental hybridisation, *Epiplatys* could not be separated from *Aplocheilus* (from Asia) and *Pachypanchax* (from islands east of the African mainland)(Scheel, 1968).

In Parenti's (1981) anatomical phylogeny of Cyprinodontiformes Berg, 1940, Aplocheiloidei comprised Aplocheilidae Bleeker, 1860 (six African and Asian genera) and Rivulidae Myers, 1925 (seven Central and South American genera). Ten specimens (from five west African collections) of *Epiplatys* were examined. *Epiplatys* was diagnosed with: posttemporal with an ossified lower limb (horizontal ramus), completely attached orbital rim,

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edentulous hypobranchials, and lacking darkened caudal margin or dorsal ocellus. The sister-group of *Epiplatys* was defined as (*Aplocheilus*, *Pachypanchax*). Synapomorphies of the three genera were: premaxilla anterodorsal process expanded, dentary coronoid process expanded, upper hypural plate bifurcate, and epibranchial 4 uncinate process absent.

The application, in systematics, of molecular sequence data, has suggested novel phylogenetic hypotheses. In an examination of aplocheiloids, Murphy and Collier (1997) sequenced 25 specimens, including three *Epiplatys* spp. The monophyly of Aplocheiloidei was supported, but Aplocheilidae (*sensu* Parenti, 1981) was paraphyletic. The relationship between *Epiplatys* and (*Aplocheilus*, *Pachypanchax*) was questioned: the sister group of *Epiplatys* was proposed to be *'Roloffia'* (from west of the 'Benin/Dahomey Gap'), which had previously been thought to be closely related to *Aphyosemion* (Nothobranchiini) (Parenti, 1981). While *Aplocheilus* and *Pachypanchax* were sister groups, (*Epiplatys*, (*Aplocheilus*, *Pachypanchax*)) formed a paraphyletic assemblage (Murphy and Collier, 1997).

Subsequently, Murphy *et al*. (1999) used three *Epiplatys* spp. as the outgroup in an analysis of 19 of the putative 22 species of *'Roloffia'*. '*Roloffia*' was defined as (*Archiaphyosemion*, (*Callopanchax*, *Scriptaphyosemion*)).

This scheme of relationships was accepted by Huber (2000) in proposing Epiplatina (comprising *Aphyoplatys*, *Epiplatys*, *Pseudepiplatys*) to be the sister group of Callopanchina (comprising *Archiaphyosemion*, *Callopanchax*, *Scriptaphyosemion*). On the basis of external morphology and reproductive ecology, *Epiplatys* was proposed to comprise eight superspecies (*Epiplatys bifasciatus*, *E. chaperi* [including *E. sangmelinensis*], *E. dageti*, *E. fasciolatus*, *E. grahami* [including *E. singa*], *E. multifasciatus*, *E. sexfasciatus* and *E. spilargyreius*) plus *Pseudepiplatys* and *Aphyoplatys*.

It is appropriate to examine relationships within *Epiplatys*, and to better define the position of *Aphyoplatys* and *Pseudepiplatys*.

MATERIALS AND METHODS

Material examined. — Institutional identification (number, and range in standard length in mm) of cleared and stained fish examined is listed for each collection. Institutional identifications: MNHN — Muséum National d'Histoire Naturelle, Paris; MRAC — Musée Royal de l'Afrique Centrale, Tervuren; USNM — United States National Museum, Washington.

Aplocheilidae. Aplocheilinae. Epiplatini. Callopanchina. *Archiaphyosemion guineense* MRAC 73-039-P-1551-1552 (2, 25-41). *Callopanchax occidentalis* MRAC 73-039-P-1671-1672 (2, 33-38). Epiplatina. *Aphyoplatys duboisi* MNHN 1981 1361 (1, 17). *Epiplatys bifasciatus* MRAC 92-059-P-2209-2210 (2, 30-36). *E. dageti* MRAC 73-039-P-2274-2275 (2, 26-35). *E. fasciolatus* MNHN 1931 0108 (2, 28-39). *E. multifasciatus* MRAC 90-047-P-864-865 (2, 24-34). *E. sangmelinensis* MNHN 1984 0593 (2, 42-48). *E. sexfasciatus* MNHN 1998 0475 (5, 20-35). *E. singa* MNHN 1998 0478 (5, 11-27); MNHN 1998 0480 (5, 14-32). *E. spilargyreius* MNHN 1981 0697 (1, 31); USNM 229818 (2, 23-28). *Pseudepiplatys annulatus* MNHN 1991 0690 (2, 21-25).

Specimens were taken from storage solutions to water, fixed for 24 h in 10% buffered formal saline then double-stained and cleared (Dingerkus and Euler, 1977). Specimens were examined with a Zeiss binocular microscope. Dissections were performed with sequential separation of the left suspensorium, left pectoral girdle, then branchial apparatus *in toto*.

Outgroup selection was based on an evaluation of relevant literature (see Discussion).

A phylogenetic analysis was performed using PAUP 3.1.1 computer software, characters were ordered with respect to the outgroup, and an exhaustive search of all possible trees undertaken (Swofford, 1993). An analysis using an unweighted pair group method with arithmetic averages (UPGMA) was also performed.

DESCRIPTIVE ANATOMY OF *EPIPLATYS SEXFASCIATUS* GILL, 1862

Type species.—*Haplocheilus sexfasciatus* Gill, 1862, by original designation.

External morphology

Body fusiform-sigmoid, head small, snout moderate, eye moderate, rarely exceeding 50 mm in SL. Mouth subterminal, large. Jaws curved, anterior angle horizontal, posterolateral portion turning posteroventrally. Upper jaw non-protracile. Upper lip short, very thick, restricted to dorsal margin of mouth. Lower lip thick, small nasal papilla projecting from upper jaw just dorsal to horizontal plane bisecting orbit, dorsal to skin flap. Dentary and premaxilla bearing 3-4 rows of small teeth, not projecting outside oral cavity.

On each side of head, two sensory pores behind eye, five sensory pores on preopercle, and two openings to nasal organ, at anterior margin of orbit. Dorsal interorbital plane with extensive, symmetrical pitting.

Single dorsal fin elongate, of anterior spur (small ray) and 9-10 rays, originating at level of transverse plane through origin of anal ray 11-12, anterior 3 rays unbranched, rays 8-10 most elongate. Anal fin elongate, of two anterior spurs and 16-17 larger rays, anterior 3-4 rays unbranched, rays 13-14 most elongate, terminating at level of dorsal ray 7-8. Caudal fin lyre-shaped, with 6-7+7 (dorsal + ventral) principal branched rays and 6-8+7 procurrent rays. Pectoral fin low-set, with dorsal spur and 15-16 branched rays. Pelvic fin on ventral body, with lateral spur and five branched rays. Anus in front of genital papilla, just anterior to origin of anal fin.

Body, including cheeks and interpelvic region, covered with cycloid scales; as many as 15 deep crenulations in largest middorsal scales. Scales in horizontal series from pectoral axilla to base of caudal fin 29-30, horizontal scale rows from origin of dorsal to anal fin 8.

Body and lower jaw black-brown, ventral surface pale. Eight or nine transverse black bars on side from head to base of tail, three or four bars traversing ventral surface. Three or four discontinuous horizontal lines of pale red spots across body. Fins dark, median fins with black edges and regular pattern of black maculi.

Live coloration variable (Scheel, 1990: 335-336). Overall blue-to-green body, incomplete red horizontal lines or dark transverse bars may be evident, fins variable.

Sexual dimorphism moderate, females and juveniles with somewhat rounded fins, devoid of red body-pigment, fins clear, transverse black bars most prominent in subadults.

Cranium

Vomer large, T-shaped, parasphenoid process attenuate, contacting ventral surface of parasphenoid (Fig. 1). Vomer anterior border convex, cluster of small teeth at ventromedial angle. Vomer anterolateral angle produced as asperity, and small process giving origin to vomeropalatine ligament, bilaterally. Biconcave meniscus interposed between dorsal surface of craniolateral angle of vomer and articular condyle of maxilla.

Parasphenoid anterior process relatively broad, somewhat cylindrical, coursing anterodorsally in median plane. Parasphenoid alar processes compact, ventral to anteromedial

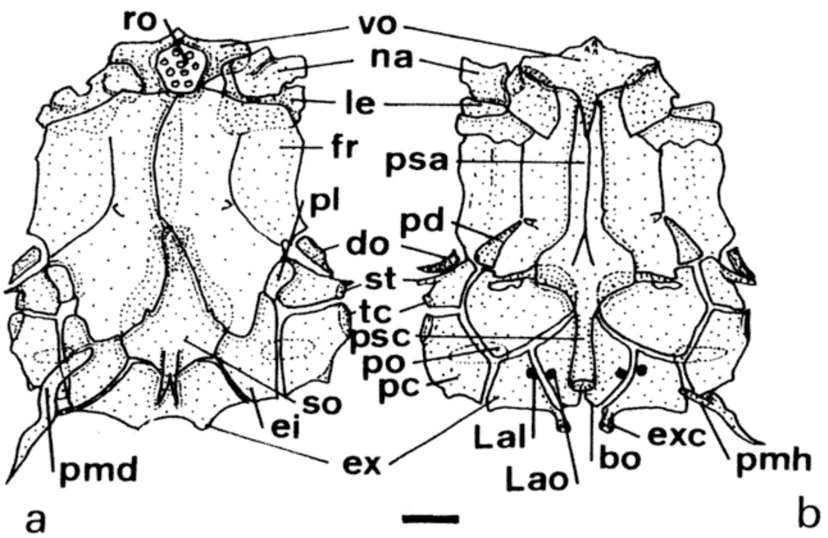


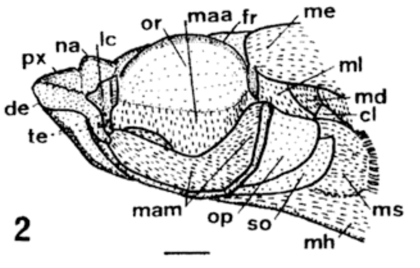
Fig. 1. *Epiplatys sexfasciatus* MNHN 1998 0475, 35 mm SL. Cranium (left posttemporal attached) in **a**: dorsal aspect; **b**: ventral aspect. Abbreviations: **bo**: basioccipital; **do**: dermosphenoid; **ei**: epiotic; **ex**: exoccipital; **exc**: exoccipital condyle; **fr**: frontal; **Lao**: origin of axialpectoral ligament; **Lal**: origin of ligament to posttemporal; **le**: lateral ethmoid; **na**: nasal; **pc**: pterotic; **pd**: pterosphenoid; **pl**: parietal; **pmd**: posttemporal dorsal ramus; **pmh**: posttemporal horizontal ramus; **po**: prootic; **psa**: parasphenoid anterior process; **psc**: parasphenoid caudal process; **ro**: rostral cartilage; **so**: supraoccipital; **st**: sphenotic; **tc**: temporal canal; **vo**: vomer. Circles: cartilage. Scale bar = 1 mm.

angle of prootics. Parasphenoid posterior process unremarkable, coursing in medial plane ventral to prootics. Basisphenoid absent. Dorsal mesethmoid discoid, occupying depression in ethmoid. Ethmoid forming anterior orbit. Dorsal mesethmoid and ethmoid cartilaginous, firmly bound together, dorsal to vomer. Ethmo-maxillary ligament originating from postero-dorsal surface of dorsal mesethmoid, bilaterally. Lateral ethmoids widely-separated about parasphenoid and vomer, forming anterior angle of orbits. Anterolateral aspect produced as condyle articulating with medial surface of palatine anterior process. Lateral ethmoid deeply invaginated anterolaterally to accommodate anterodorsal portion of palatine, deep to nasal organ.

Rostral cartilage pentagonal, anterior margin broad, dorsal surface convex, ventral surface concave, dorsal to ethmoid. Rostral cartilage anteroventrally attached to premaxilla dorsomedial angle. Ventral surface giving origin to ligament attached to medial angle of maxilla anterior process.

Nasal small, approximately quadrilateral, contacting upper lip anteriorly, frontal posteriorly, firmly bound to dorsal mesethmoid medially, lachrymal and lateral ethmoid ventrally. Frontals broad, median synthesis approximately symmetric, precluding fontanel. Frontal supraorbital lamina concave in ventral aspect (Fig. 2), separated from median lamina by shallow curved sulcus. Poorly-developed transverse inscription dividing median lamina approximately in half, posterior portion forming part of calvarium. Parietal well-developed, reniform, partially covered by posterolateral angle of frontal, dorsal to sphenotic.

Supraoccipital approximately diamond-shaped (in dorsal aspect), with deltoid anterior process deep to junction of frontals, forming posterior calvarium. Supraoccipital contacting



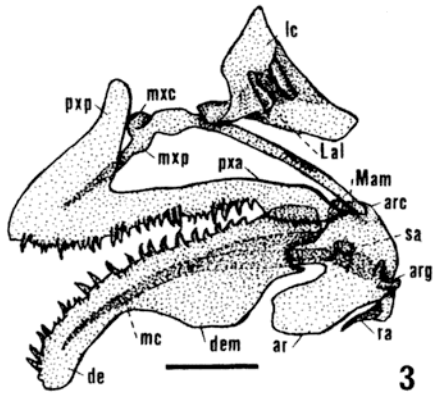


Fig. 2. – Same specimen. Superficial musculature of the head and pectoral region, eye removed. Abbreviations: **cl**: cleithrum; **de**: dentary; **fr**: frontal; **lc**: lachrymal; **maa**: muscle *adductor arcus palatini*; **mam**: muscle *adductor mandibulae*; **md**: muscle *adductor profundus*; **me**: epaxial musculature; **mh**: hypaxial musculature; **ml**: muscle *levator operculi*; **ms**: muscle *abductor superficialis*; **op**: opercle; **or**: orbit; **px**: premaxilla; **te**: tendons from *adductor mandibulae* to medial surface of lachrymal and maxilla. Dotted lines: obscured structures. Scale bar = 1 mm.

Fig. 3. – Same specimen. Jaws and lachrymal in lateral aspect. Abbreviations: **ar**: articular; **arg**: articular glenoid cavity; **arc**: articular coronoid process; **de**: dentary; **dem**: dentary posteromedial process; **Lal**: insertion of tendon of adductor musculature to lachrymal; **lc**: lachrymal; **Mam**: insertion of adductor musculature on maxilla; **mc**: mandiblar cartilage; **mxc**: maxillary condyle; **mxp**: maxilla ventral process; **pxa**: premaxilla alveolar ramus; **pxp**: premaxilla anterodorsal process; **ra**: retroarticular; **sa**: supraangular. Dotted lines: obscured structures. Scale bar = 1 mm.

epiotics caudolaterally, exoccipitals caudoventrally. Supraoccipital crest well-developed, divided in median plane.

Pterosphenoid deltoid, at posterodorsal area of lateral margin of orbit, contacting frontal dorsally and sphenotic posteriorly. Sphenotic ovoid, at posterior angle of orbit. Sphenotic bearing large postorbital process, anterior facet of process contacting dermosphenoid anterior to facet for hyomandibular. Pterotic forming caudolateral angle of cranium, contacting sphenotic anteriorly, exoccipital posteriorly, and basioccipital ventrally. Pterotic lateral margin produced as small ventrally-directed process. Temporal canal spanning sphenotic and pterotic, giving origin to muscle *levator operculi*. Hyomandibular dorsal surface interposed between ventral processes of sphenotic and pterotic.

Epiotic forming posterolateral portion of calvarium. Vertical ridge of epiotic contacting dorsal ramus of posttemporal. Temporal fossa bound by sphenotic anteriorly, pterotic ventrally, and epiotic caudally, providing insertion for substantial portion of epaxial musculature.

Exoccipitals at posterior angle of cranium, median synchondrosis dorsal to foramen magnum, ventral to supraoccipital. Exoccipital posteroventral angle produced as minor occipital condyle. Ligament to post-temporal originating from ventral surface of exoccipital. Intercalar absent.

Prootics approximately pentagonal, contributing to floor of cranial vault. Prootic median synchondrosis lying dorsal to parasphenoid. Basioccipital approximately diamond-shaped, posterior angle produced as major occipital condyle, ventral to foramen magnum. Axialpectoral (Baudelot's) ligament originating from basioccipital ventral surface, bilaterally.

Basioccipital dorsal surface joined bilaterally to exoccipitals by vertical osseous trabeculae, forming partition between otoliths and brain stem.

Otic bulla shallow, formed by prootic anteriorly, pterotic laterally, exoccipital and basioccipital posteriorly. Sagitta and asterix resting in otic bulla, covered dorsolaterally by cavernous expansion of epiotic and exoccipital.

Jaws

Maxilla irregular, tubiform, anterior ramus extending anteromedially deep to premaxilla anterodorsal process (Fig. 3). Anterior angle attached ligamentously to ventral surface of premaxilla anterodorsal process posterior angle. Prominent dorsolateral condyle forming, with maxilla anterodorsal process, sulcus for premaxilla anterior process. Ventral to condyle, small maxillary process extending external to premaxilla, receiving ethmo-maxillary ligament. Lateral to condyle, palatine anterodorsal process attached by palato-maxillary ligament. Maxilla caudolateral ramus elongate, receiving tendon from muscle *adductor mandibulae* towards distal angle.

Premaxilla with broad, tapering anterodorsal process. Premaxilla alveolar ramus narrow, with 2-3 rows of caniniform teeth, larger teeth placed distally. Dental series terminating at posterior expansion of premaxilla. Premaxilla terminating in narrow posterior process.

Dentary curved, narrow, anterior two-thirds bearing 3-4 rows of caniniform teeth, posteromedial portion produced as large process, edentulous. Articular comprising elongate dorsal, and ovoid ventral, portions. Anterodorsal process coursing on internal surface of base of dentary. Articular coronoid process low. Posteromedial angle of articular produced as trochlea, bearing glenoid cavity, for articulation with quadrate tubercle. Retroarticular irregular, elongate, tapering anteroventrally, at caudoventral angle of articular. Mandibular (Meckel's) cartilage originating from caudal angle of articular, coursing on medial surfaces of articular and dentary to termination deep to anterior synthesis of contralateral dentaries. Supraangular (coronomeckelian) small, irregular, on dorsal surface of caudal angle of mandibular cartilage, acting as insertion for mandibular adductor musculature.

Suspensorium

Palato-quadrate assemblage narrow, edentulous. Palatine elongate, anterior angle capped with cartilage, lying ventral to nasal, lateral to lateral ethmoid, dorsal to maxilla, and medial to lachrymal. Palatine posteroventral border contacting dorsal margin of laminar palato-quadrate cartilage, posteroventrally contacting quadrate. Endopterygoid arcuate, coursing along posterior margin of palato-quadrate. Ectopterygoid absent.

Quadrate with sector-like anterior segment and narrow posterolateral preopercle ramus, separated by symplectic incisure. Quadrate lateral ramus bearing prominent anterolateral tubercle, forming ginglymus with trochlea of articular. Symplectic elongate, laminar, contacting quadrate anteroventrally, metapterygoid dorsally, and hyomandibular posteriorly. Interhyal ligament attached to medial face of synchondrosis between symplectic and hyomandibular. Metapterygoid narrow, elongate, contacting dorsal border of symplectic.

Hyomandibular stellate, at caudal margin of orbit. Hyomandibular dorsal margin bearing two condyles articulating with facets of sphenotic and pterotic. Hyomandibular anteroventral margin contacting symplectic and metapterygoid, caudal margin bearing tubercle for articulation with opercle, dorsal to termination of preopercle vertical ramus.

Preopercle of two perpendicular rami forming rightangular trough open ventrally and caudally. Larger portion of muscle *adductor mandibulae* originating from angle enclosed by preopercle (Fig. 3). Preopercle horizontal ramus greater than vertical ramus, anterodorsal angle with laminar ossification. Preopercle superficial to other suspensorial elements.

Opercular series

Interopercle approximately deltoid, with dorsal notch adjacent to epihyal caudodorsal angle. Medial face of interopercle (and subopercle) joined to branchiostegal rays in hyoid musculature. Opercle deltoid, horizontal axis greater then vertical axis. Anterodorsal angle bearing dorsal process for insertion of muscle *dilator operculi*, and forming process with glenoid cavity, articulating with hyomandibular. Anterior border bearing two approximately-parallel inscriptions demarcating contact with hyomandibular medial face. Subopercle irregular, with prominent anterodorsal process deep to preopercle, and lachrymiform posterodorsal process deep to caudal margin of opercle.

Circumorbital series

Lachrymal approximately deltoid, apex directed ventrally, vertical axis elongate. Lateral face bearing open, vertical sensory canal, towards caudal border. Medial face bearing small process receiving tendon from muscle *adductor mandibulae*. Dermosphenoid on anterior face of sphenotic process, forming small narrow trough open laterally. Eye with two scleral ossicles (in larger specimens), anterior element adjacent to lateral ethmoid, posterior element adjacent to dermosphenoid.

Hyobranchial apparatus

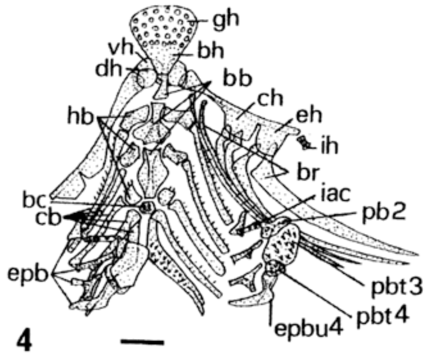
Basihyal broad (Fig. 4), anteriorly fused to spatulate, expansive glossohyal cartilage, both elements edentulous. Basihyal caudally articulating with first basibranchial, caudolaterally bearing large condyles articulating with dorsal hypohyal. First basibranchial small, second basibranchial with posterior expansions, third basibranchial largest, dorsally contacting cartilaginous nodule lying in horizontal basibranchial plane.

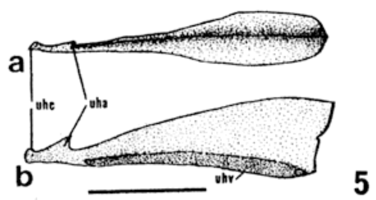
Urohyal deltoid in lateral aspect (Fig. 5). Urohyal anterior condyle attached ligamentously to ventral hypohyals, small anterodorsal process ventral to basihyals, urohyal ventral border forming open canal. Dorsal hypohyal small, pyramidal, contacting larger, irregular, ventral hypohyal (Fig. 4), produced as anterior process receiving ligament from urohyal. Ceratohyal irregular, conical anterior portion, articulating with hypohyal, joined by narrow collus to expansive quadrilateral lamina. Ceratohyal and epihyal joined along vertical synchondrosis, reinforced dorsally with osseous anastomosis. Epihyal quadrilateral, dorsal border horizontal, posterior border directed dorsally. Posterodorsal angle giving origin to interhyal ligament, inserting on medial face of synchondrosis between hyomandibular and symplectic. Small barbel-shaped interhyal formed in ligament, close to epihyal.

Two small, anterior branchiostegals contacting ventral margin of ceratohyal collus. Two large, lamellar branchiostegals contacting lateral face of body of ceratohyal, two posterior branchiostegals contacting epihyal.

First hypobranchial pentagonal. Hypobranchials 2 and 3 smaller, near-discoid.

Anterior three ceratobranchials elongate, slightly curved, conical anterior angles contacting posterior border of respective hypobranchial. First ceratobranchial anterior surface bearing nine gill rakers, distal gill rakers cartilaginous. Ceratobranchial 4 contacting basibranchial cartilaginous nodule. Ceratobranchial 5 sigmoid, anteriorly united to fellow via strong median syndesmosis. Anterior angle of ceratobranchial 5 contacting anterior angle of ceratobranchial 4. Ceratobranchial 5 dorsal surface dentigerous, with large caniniform teeth at medial margin. Ventral surface with large muscular process, distal angle produced as muscular process.





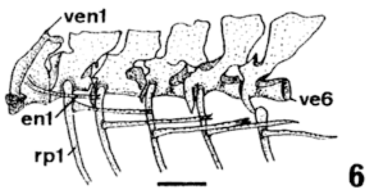


Fig. 4. – Same specimen. Hyobranchial apparatus in dorsal aspect, right pharyngobranchials teased open, left branchiostegals removed. Abbreviations: **bb**: basibranchial; **bc**: basibranchial cartilage; **bh**: basihyal; **br**: branchiostegal; **cb**: ceratobranchial; **ch**: ceratohyal; **dh**: dorsal hypohyal; **eh**: epihyal; **epb**: epibranchial; **epbu**: epibranchial 4 uncinate process; **gh**: glossohyal cartilage; **hb**: hypobranchial; **iac**: interarcual cartilage; **ih**: interhyal; **pb**: pharyngobranchial; **pbt**: pharyngobranchial toothplate; **vh**: ventral hypohyal. Circles: cartilage. Scale bar = 1 mm.

Fig. 5. – Same specimen. Urohyal in **a**: dorsal aspect; **b**: left lateral aspect. Abbreviations: **uha**: urohyal anterodorsal process; **uhc**: urohyal condyle; **uhv**: urohyal ventral canal. Scale bar = 1 mm.

Fig. 6. – Same specimen. First six precaudal vertebrae. Abbreviations: **en**: epineural; **rp**: pleural rib; **ve**: vertebra; **ven**: vertebral neural process. Scale bar = 1 mm.

First epibranchial cartilaginous in most specimens, proximal angle broad, bearing two rudimentary gill-rakers, base contacting ceratobranchial 1, apex directed dorsally. Interarcual cartilage from base of epibranchial 1 to dorsal margin of pharyngobranchial 2. Epibranchials 2 and 3 elongate, with broad base contacting respective ceratobranchial, apex contacting respective pharyngobranchial. Epibranchial 4 large, angular, coursing from distal angles of ceratobranchials 4 and 5 to posterodorsal aspect of pharyngobranchial 3. Epibranchial 4 uncinate process poorly developed. Pharyngobranchial 2 irregular-lamellar, dentigerous. Pharyngobranchial 3 large, ovoid, ventral surface bearing two pharyngobranchial toothplates with large caniniform teeth, posteroventral angle bearing small fourth toothplate.

Vertebrae and ribs

Total vertebrae 29-30, precaudal 13, caudal 16-17. First vertebra with small paired anteroventral condyles articulating with exoccipital condyles, and small bifid neural process. Neural processes of vertebrae 2-6 broad (Fig. 6). Neural processes of remaining vertebrae spinous, tallest spine at origin of dorsal fin. Anterior dorsal zygapophyses prominent from second to last precaudal vertebrae, much-reduced in caudal vertebrae. Posterior dorsal, anterior ventral and posterior ventral zygapophyses undeveloped.

Precaudal vertebrae bearing large laterally-directed parapophyses, directed ventrally in last two precaudal vertebrae, developed as haemal arches in first 1-2 caudal vertebrae, as haemal spines in remaining caudal vertebrae. Dorsal angle of pleural ribs contacting posterior surface of parapophyses from second to last precaudal vertebrae. Epineurals associated with all precaudal vertebrae, originating from parapophysis of first vertebra and dorsal angle of pleural ribs. First 4-6 epineurals with broad or bifid distal angles (Parenti, 1981) in some specimens.

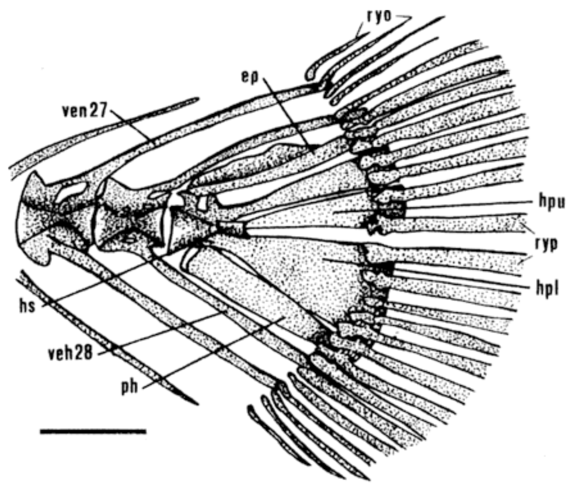


Fig. 7. – Same specimen. Caudal skeleton. Abbreviations: **ep**: epural; **hpl**: lower hypural plate; **hpu**: upper hypural plate; **hs**: hypurapophysis; **ph**: parhypural; **ryo**: procurrent ray; **ryp**: principal ray; **veh**: vertebral haemal spine; **ven**: vertebral neural process. Stippling: cartilage. Scale bar = 1 mm.

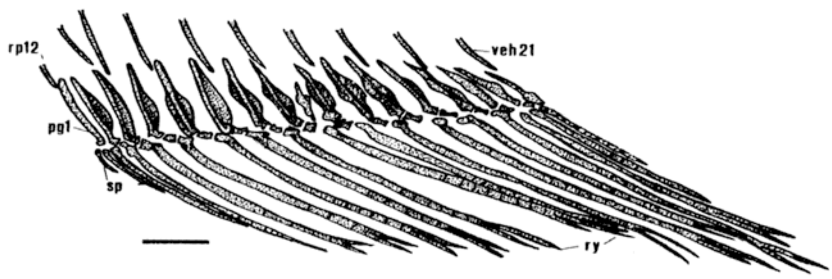


Fig. 8. – Same specimen. Anal fin and supports. Abbreviations: **pg**: pterygiophore; **rp**: pleural rib; **ry**: fin ray; **sp**: fin spur; **veh**: vertebral haemal spine. Scale bar = 1 mm.

Caudal skeleton near-symmetric (Fig. 7). Single narrow epural opposite narrow autogenous parhypural. Uroneural and urostyle absent. Upper and lower hypural plates about horizontal fissure, upper hypural plate bifid in most specimens. Hypurapophysis just below horizontal plane through vertebral centrae. Preural radial cartilage absent.

Fins and girdles

Dorsal fin originating at level of transverse plane through vertebra 20, terminating at level of vertebra 24. Anterior spur and adjacent ray supported on broad pterygiophore (formed by fusion of two elements prior to maturity), subsequent rays supported individually by narrow, similar-size pterygiophores except small terminal non-supportive element.

Anal fin commencing at level of vertebrae 13-14 (Fig. 8), terminating at level of vertebrae 23-24. Anterior two spurs and adjacent ray supported by single pterygiophore,

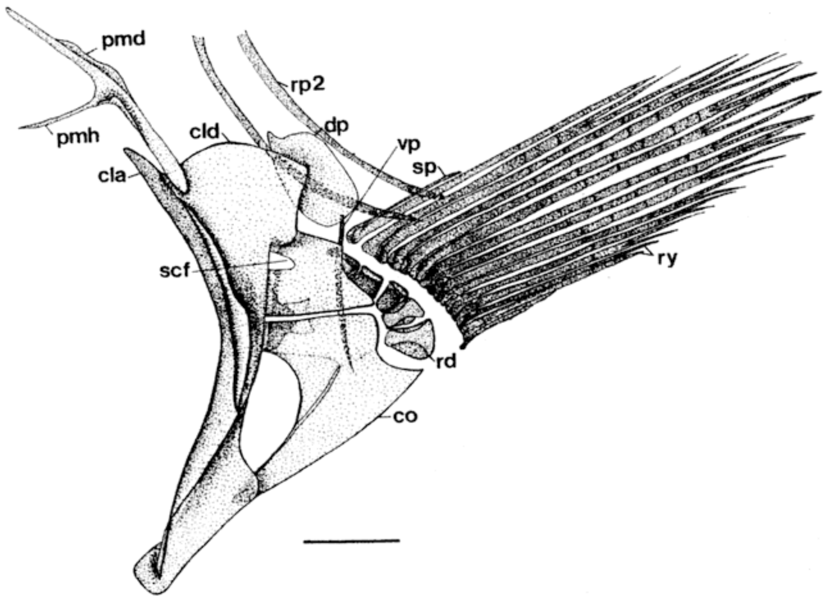


Fig. 9. — Same specimen. Pectoral girdle. Abbreviations: **cla**: cleithrum anterodorsal spine; **cld**: cleithrum posterodorsal process; **co**: coracoid; **dp**: dorsal postcleithrum; **pmd**: posttemporal dorsal ramus; **pmh**: posttemporal horizontal ramus; **rd**: proximal radial; **rp**: pleural rib; **ry**: fin ray; **scf**: scapula foramen; **sp**: fin spur; **vp**: ventral postcleithrum. Scale bar = 1 mm.

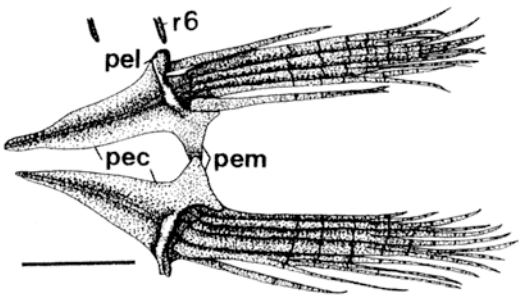


Fig. 10. — Same specimen. Pelvic fin in dorsal aspect. Abbreviations: **pec**: pelvic anterior spinous process; **pel**: pelvic dorsolateral process; **pem**: pelvic medial process; **r6**: distal angle of sixth pleural rib. Scale bar = 1 mm.

subsequent rays supported by individual pterygiophores. Anterior three pterygiophores increasing in size, subsequent pterygiophores approximately equal except terminal smaller element (not supporting a ray in some specimens).

Pectoral fin irregular, low-set, obliquely-oriented, largely below horizontal plane bisecting orbit. Cleithrum elongate, twisted. Anterior margin retrorse (Fig. 9), forming trough giving origin to muscle *abductor superficialis* (Fig. 2). Axial-pectoral (Baudelot's) ligament inserting on anterior aspect of dorsal spinous process, anterior to moderate posterodorsal process. Cleithrum anteroventral angle drawn into moderate process (Fig. 9) contacting contralateral structure about small spherical intercleithral cartilage, at level of transverse plane through preopercle vertical ramus.

Scapula approximately quadrilateral, horizontal axis greater than vertical axis, large obliquely-oriented foramen progressively ossifying during maturation. Anterior margin embedded in trough of cleithrum, posterior margin supporting spur and first few rays, indented for first proximal radial and portion of second radial. Coracoid approximately deltoid, anterior margin curved, posterior margin scalloped to accommodate third and fourth proximal radials. Proximal radials compact, quadrilateral, increasing in size from dorsal to ventral. Muscle *adductor profundus* inserting on medial face of coracoid (Fig. 2).

Post-temporal elongate, obtusely angled, dorsal ramus contacting epiotic, ventral ramus forming thin ossification in ligament attaching to exoccipital (Fig. 9). Supracleithrum fused to posttemporal (Parenti, 1981). Dorsal postcleithrum small, ovoid, deep to cleithrum posterodorsal process, in first intercostal space. Ventral postcleithrum small, on anterior aspect of first pleural rib.

Pelvic fin elongate (Fig. 10), on belly, in transverse plane of vertebrae 8-11. Medial lamina narrow-deltoid, contacting contralateral structure anteriorly, diverging posteriorly. Posteromedial process overlapping somewhat asymmetric contralateral structure. Dorsolateral process in fifth intercostal space, attached to sixth pleural rib by weak ligament. Small posterior spine dorsal to medial pelvic ray.

CHARACTERS

1. Origin of dorsal fin

The dorsal fin originates anterior to a transverse plane through the origin of the anal fin in *Callopanchax occidentale*, about one-third of the length of the anal fin in *Archiaphyosemion guineense*, and about half the length of the anal fin in *Aphyoplatys*. The dorsal originates posterior to midway along the anal fin in the remaining taxa. (**0** = origin of dorsal relatively anterior; **1** = origin of dorsal posterior).

2. Width of parasphenoïde

The anterior ramus of the parasphenoid is somewhat narrow in most taxa (Fig. 11a, 11b), but relatively broad in *Epiplatys dageti*, *E. fasciolatus* (Fig. 11c) and *E. sexfasciatus*. (**0** = parasphenoid anterior ramus moderate; **1** = parasphenoid anterior ramus broad).

3. Shape of rostral cartilage

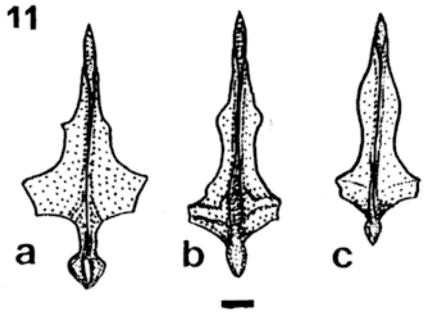
The rostral cartilage is discoid in *A. guineense*, *C. occidentale* and *Pseudepiplatys* (Fig. 12c). In other taxa (Fig. 12a, 12b) it is pentagonal. (**0** = rostral cartilage discoid; **1** = cartilage pentagonal).

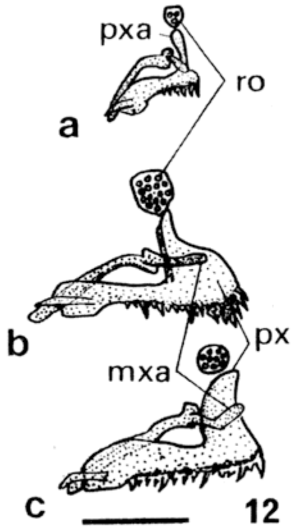
4. Shape of maxilla anterior ramus

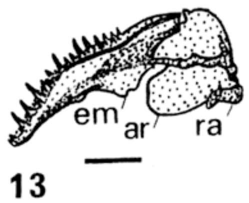
The anterior ramus of the maxilla is relatively straight in all taxa (Figs 3, 12a, 12b) except *Pseudepiplatys*, in which it is curved (Fig. 12c). (**0** = maxilla anterior ramus straight; **1** = ramus curved).

5. Shape of premaxilla

The anterodorsal process of the premaxilla is relatively broad, the dorsal angle being produced as a narrow point in all taxa except *Aphyoplatys* (Fig. 12a) and *Pseudepiplatys* (Fig. 12c), in which dorsal angle is not markedly narrow. (**0** = premaxilla dorsal angle narrow; **1** = premaxilla without narrow dorsal angle).







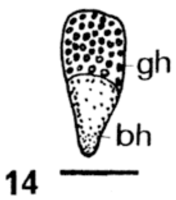


Fig. 11. Parasphenoids in ventral aspect of **a**: *Archiaphyosemion guineense* MRAC 73-039-P-1551, 41 mm SL; **b**: *Epiplatys sangmelinensis* MNHN 1984 0593, 48 mm SL; **c**: *Epiplatys fasciolatus* MNHN 1931 0108, 39 mm SL. Scale bar = 1 mm.

Fig. 12. Rostral cartilage, maxilla and premaxilla in medial aspect of **a**: *Aphyoplatys duboisi* MNHN 1981, 17 mm SL; **b**: *Epiplatys singa* MNHN 1998 0478, 27 mm SL; **c**: *Pseudepiplatys annulatus* MNHN 1991 0690, 25 mm SL. Abbreviations: **mxa**: maxilla anterior ramus; **px**: premaxilla; **pxa**: premaxilla anterodorsal process; **ro**: rostral cartilage. Circles: cartilage. Scale bar = 1 mm.

Fig. 13. *Epiplatys fasciolatus* MNHN 1931 0108, 39 mm SL. Lower jaw in lateral aspect. Abbreviations: **ar**: articular; **em**: dentary posteromedial process; **ra**: retroarticular. Scale bar = 1 mm.

Fig. 14. *Epiplatys dageti* MRAC 73-039-P-2274, 35 mm SL. Basihyal and glossohyal in dorsal aspect. Abbreviations: **bh**: basihyal; **gh**: glossohyal. Circles: cartilage. Scale bar = 1 mm.

6. Size of dentary posteromedial process

There is a moderate process arising on the ventral aspect of the dentary (Fig. 13) of some taxa. It is markedly enlarged in *Aphyoplatys*, *E. dageti*, *E. multifasciatus*, *E. sexfasciatus* (Fig. 3) and *Pseudepiplatys*. (**0** = dentary ventromedian process moderate; **1** = process large).

7. Length of retroarticular

The retroarticular is of moderate length in all taxa (Fig. 13) except *E. sexfasciatus* (Fig. 3) and *E. singa*, in which it is elongate. (**0** = retroarticular moderate; **1** = retroarticular elongate).

8. Width of basihyal and glossohyal

The basihyal and glossohyal are broad in all taxa (Fig. 4) except *Aphyoplatys*, *E. bifasciatus*, *E. dageti* (Fig. 14) and *Pseudepiplatys*, in which it is relatively narrow. (**0** = basihyal broad; **1** = basihyal narrow).

9. Width of base of epibranchial 1

Epibranchial 1 has a broad base in all taxa except *Aphyoplatys*, *E. singa* (Fig. 15) and

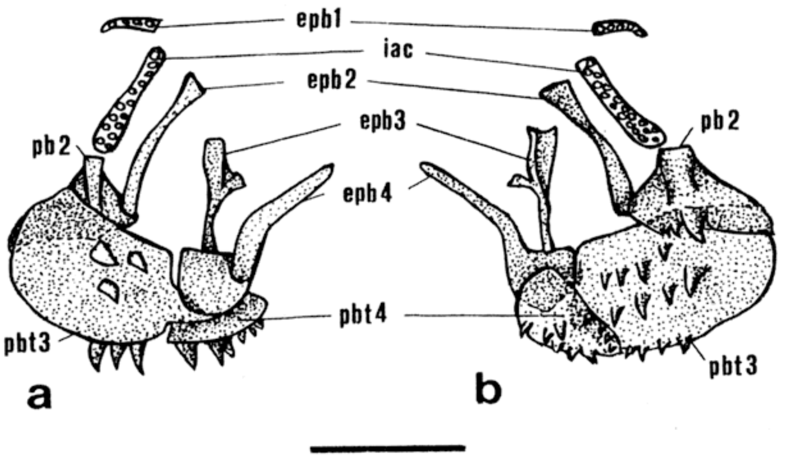


Fig. 15. *Epiplatys singa* MNHN 1998 0478, 35 mm SL. Right epibranchials and pharyngobranchials in **a**: dorsal aspect; **b**: ventral aspect. Abbreviations: **epb**: epibranchial; **iac**: interarcual cartilage; **pb**: pharyngobranchial; **pbt**: pharyngobranchial toothplate. Circles: cartilage. Scale bar = 1 mm.

Pseudepiplatys (Fig. 16), in which it is markedly narrow. (**0** = epibranchial 1 base broad; **1** = base narrow).

10. Width of epibranchial 3

Epibranchial 3 has a broad base in all taxa (Figs 4, 15) except *Aphyoplatys* and *Pseudepiplatys* (Fig. 16), in which it is narrow. (**0** = epibranchial 3 base broad; **1** = base narrow).

11. Development of epibranchial 4 uncinate process

A distinct uncinate process is present on epibranchial 4 in all taxa (Fig. 16) except *Aphyoplatys*, *E. sangmelinensis*, *E. sexfasciatus* (Fig. 4) and *E. spilargyreius*, in which it is poorly developed. (**0** = epibranchial 4 uncinate process distinct; **1** = process undistinguished).

12. Size of interarcual cartilage

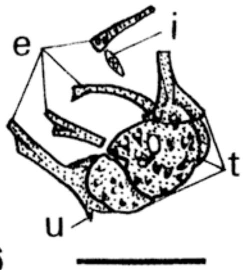
A large interarcual cartilage between epibranchial 1 and the second pharyngobranchial toothplate is present in all taxa (Figs 4, 15) except *Pseudepiplatys* (Fig. 16), in which it is markedly reduced. (**0** = interarcual cartilage large; **1** = cartilage small).

13. Structure of hypural plate

The hypural plate comprises separate upper and lower elements (Fig. 7) except in *Aphyoplatys*, in which the plate comprises a single fused element (Fig. 17). (**0** = hypural plate of upper and lower elements; **1** = plate a single fused element).

14. Structure of post-temporal

The posttemporal has ossified dorsal and horizontal rami in all taxa (Fig. 9) except *Aphyoplatys* and *Pseudepiplatys* (Fig. 18), in which the horizontal ligament to the exoccipital does not ossify. (**0** = post-temporal with ossified horizontal ramus; **1** = horizontal ligament present).



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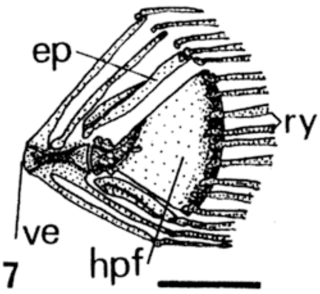

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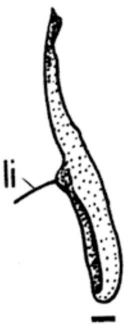

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Fig. 16. *Pseudepiplatys annulatus* MNHN 1991 0690, 25 mm SL. Right epibranchials and pharyngobranchials in ventral aspect. Abbreviations: **e**: epibranchial; **i**: interarcual cartilage; **t**: phayngobranchial toothplate; **u**: epibranchial 4 uncinate process. Circles: cartilage. Scale bar = 1 mm.

Fig. 17. *Aphyoplatys duboisi* MNHN 1981 1361, 17 mm SL. Caudal skeleton. Abbreviations: **ep**: epural; **hpf**: hypural plate; **ry**: principal ray; **ve**: vertebra 25. Stippling: cartilage. Scale bar = 1 mm.

Fig. 18. *Pseudepiplatys annulatus* MNHN 1991 0690, 25 mm SL. Posttemporal in lateral aspect. Abbreviation: **li**: ligament to exoccipital. Scale bar = 0.1 mm.

15. Attachment of pelvis to pleural rib

The dorsolateral process of the pelvic fin lies in the seventh intercostal space, and is attached ligamentously to the ventral angle of the eighth pleural rib, in *A. guineense* and *C. occidentale*. The fin is in the sixth intercostal space, attaching to the seventh rib, in *E. spilargyreius*. In the other taxa the fin is in the fifth intercostal space, attaching to the sixth rib (Fig. 10). (**0** = pelvis to rib 8 or 7; **1** = pelvis to rib 6).

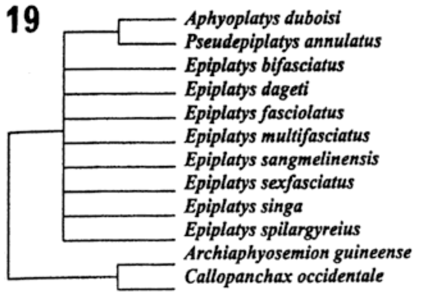
16. Width of epineurals

The epineurals have a relatively broad distal (free) angle in all taxa (Fig. 6) except *Pseudepiplatys*, in which the epineurals are relatively narrow. (**0** = epineurals relatively broad; **1** = epineurals narrow).

The data matrix for these characters is reproduced in table I.

Table I. Character data matrix for an analysis of two outgroups and ten Epiplatina spp.

Species Character	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Archiaphyosemion guineense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Callopanchax occidentale	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aphyoplatys duboisi	0	0	1	0	1	1	0	1	1	1	1	0	1	1	1	0
Epiplatys bifasciatus	1	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0
Epiplatys dageti	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0
Epiplatys fasciolatus	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Epiplatys multifasciatus	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0
Epiplatys sangmelinensis	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0
Epiplatys sexfasciatus	1	1	1	0	0	1	1	0	0	0	1	0	0	0	1	0
Epiplatys singa	1	0	1	0	0	0	1	0	1	0	0	0	0	0	1	0
Epiplatys spilargyreius	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Pseudepiplatys annulatus	1	0	0	1	1	1	0	1	1	1	0	1	0	1	1	1



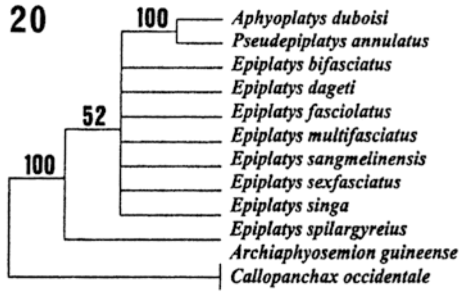


Fig. 19. Phylogenetic analysis of Epiplatina. Strict consensus analysis of 789 most-parsimonious trees generated by PAUP analysis of two outgroups and ten Epiplatina species.

Fig. 20. Phylogenetic analysis of Epiplatina. 50% majority rule analysis of 789 most-parsimonious trees generated by PAUP analysis of two outgroups and ten Epiplatina species. Numbers represent the percentage of trees in which groupings were supported.

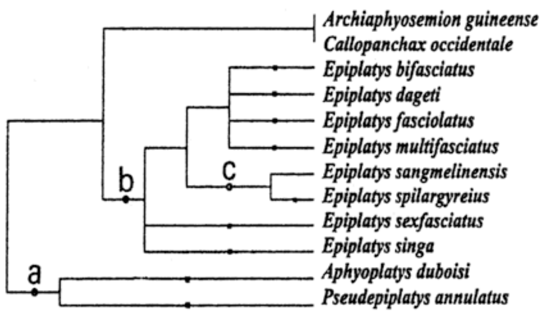


Fig. 21. UPGMA analysis of two outgroups and ten Epiplatina species. Key to advanced character states (and one reversal) of nodes and species. **a**: characters **5, 6, 8, 9, 10, 12, 14** and **15**; **b**: characters **1, 3** and **15**; **c**: character **11**; *Epiplatys bifasciatus*: character **8**; *Epiplatys dageti*: characters **2, 6** and **8**; *Epiplatys fasciolatus*: character **2**; *Epiplatys multifasciatus*: character **6**; *Epiplatys sangmelinensis*: no apomorphies; *Epiplatys spilargyreius*: character **15** reversal; *Epiplatys sexfasciatus*: characters **2, 6** and **11**; *Epiplatys singa*: characters **7** and **9**; *Aphyoplatys duboisi*: characters **3, 11** and **13**; *Pseudepiplatys annulatus*: characters **1, 4, 12** and **16**.

ANALYSES

Phylogenetic analysis of the data matrix found 789 most-parsimonious trees (length = 26 steps). Strict consensus resulted in a tree (consistency index = 0.6154, retention index = 0.5833) with an in-group polytomy unresolved except for the placement of *Aphyoplatys* and *Pseudepiplatys* as sister groups (Fig. 19). The 50% majority-rule consensus tree depicted *E. spilargyreius* as the sister group of the other Epiplatina species (Fig. 20).

Analysis using UPGMA provided more resolution, with a polytomy comprising (*E. bifasciatus*, *E. dageti*, *E. fasciolatus*, *E. multifasciatus*) as a sister group of (*E. sangmelinensis*, *E. spilargyreius*). This group was in turn part of a trichotomy with *E. sexfasciatus* and *E. singa*. This group was a sister group of Callopanchina. (*Aphyoplatys*, *Pseudepiplatys*) was the group most distantly related to the other taxa (Fig. 21).

DISCUSSION

In selecting an outgroup for this study, evidence of the vicariance and genetic distance (Murphy and Collier, 1997) between Epiplatina, Callopanchina and (*Aplocheilus*, *Pachypanchax*) was taken into account. However, the possible paraphyly of *Archiaphyosemion* (Murphy *et al.*, 1999), and the possibility that Callopanchina evolved after speciation in *Epiplatys*, cannot be discounted.

The hypothesised sister group relationship, and relatedness to *Epiplatys*, of *Aphyoplatys* and *Pseudepiplatys* requires further clarification. The localities of the monotypic genera are separated by the 'Benin/Dahomey gap'. While it is possible that *Aphyoplatys* and *Pseudepiplatys* represent isolated remnants of stock ancestral to present-day *Epiplatys*, it is also possible that the monotypic genera evolved separately from *Epiplatys*-like forms through convergent morphological processes. There is thus a possibility that *Aphyoplatys* and/or *Pseudepiplatys* may be the sister group of (Callopanchina, *Epiplatys*).

Twelve shared characters (**1, 2, 3, 5, 6, 7, 8, 9, 10, 11, 14** and **15**) were used to generate the PAUP analyses, which were largely uninformative. Monophyly of (*Aphyoplatys*, *Pseudepiplatys*) was well-supported (present in 100% of most-parsimonious trees) but separation of *E. spilargyreius* from other Epiplatina species was poorly supported (52%)(Fig. 10).

The UPGMA analysis provided deeper resolution, proposing (*E. bifasciatus*, *E. dageti*, *E. fasciolatus*, *E. multifasciatus*) as a sister group of (*E. sangmelinensis*, *E. spilargyreius*). *Epiplatys sexfasciatus* and *E. singa* were somewhat distinct. It has been suggested that (*E. bifasciatus*, *E. fasciolatus*, *E. spilargyreius*, *E. singa*) form a monophyletic assemblage, and that (*E. sangmelinensis*, *E. spilargyreius*) may be a superspecies (Huber, 2000). That proposal has some similarity with the present result. However, as the UPGMA methodology used here does not have a phylogenetic basis, this result may not be widely accepted.

Synapomorphic for *Aphyoplatys* and *Pseudepiplatys* were advanced states of three characters (**5**, **10** and **14**), two of which (epibranchial 3 base narrow, posttemporal horizontal ramus not ossified) could be interpreted as the result of paedomorphism. Paedomrphism - the retention, in adults of one species, of features present in sub-adult stages of another closely-related species - can confound morphological analyses. Autapomorphic for *Aphyoplatys* was character **13**, while characters **4, 12** and **16** were autapomorphic for *Pseudepiplatys*. Fusion of the hypural plate (character **13**), reduction of the interarcual cartilage (character **12**) and narrow epineurals (character **16**) could also be interpreted as paedomorphism.

Examination of developmental sequences, from egg to maturity, would be invaluable in the further evaluation of aplocheiloid phylogenetics. The present hypotheses will provide a point of reference for further morphological studies, and molecular studies (if suitably-preserved material can be obtained).

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