The skull of the gymnophthalmid lizard *Neusticurus ecpleopus* (Reptilia: Squamata)

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We provide a detailed description of the hyoid apparatus and cranial osteology of the gymnophthalmid lizard *Neusticurus ecpleopus*, based on a series of 11 dry skeletal preparations and 22 cleared and double-stained specimens. Articulated and disarticulated material permit detailed descriptions of isolated bones as well as the overall architecture of the skull. Individual and ontogenetic variation within *N. ecpleopus* is discussed. The greatest intraspecific variation is reflected in features that vary during ontogeny, including firmness of articulation between bones of the dermatocranium, thickness of individual bones, degree of elongation or expansion of processes, relative width of the parietal table, elongation of the hyoid apparatus, lateral angulation of the first ceratobranchial and relatively late appearance of the second ceratobranchial. The skull of *N. ecpleopus* can be regarded as generally representative of the Gymnophthalmidae, but we provide preliminary discussion of areas where variation in gymnophthalmid skull configuration is pronounced.   © 2003 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2003, **139**, 283–304.

ADDITIONAL KEYWORDS: cranial osteology – Gymnophthalmidae – hyoid apparatus – ontogeny – South America – variation.

INTRODUCTION

Gymnophthalmidae is a diverse group of Central and South American squamate reptiles currently thought to be the sister group of the Teiidae (Estes, de Queiroz & Gauthier, 1988; Schwenk, 1988; Evans & Barbadillo, 1997, 1998; Evans & Chure, 1998; Caldwell, 1999). The group accommodates approximately 170 currently recognized species in 36 genera, but it remains one of the most poorly known of all squamate clades, and many aspects of gymnophthalmid anatomy, physiology, systematics and ecology are poorly understood.

The history of classification of gymnophthalmid and teiid lizards is long and complex. Most recent classifications can be traced back to Boulenger (1885), who placed these diverse lizards in a single family (Teiidae), and established four morphologically

distinct groups. Boulenger's Group I included the relatively large-bodied forms, *Ameiva*, *Callopistes*, *Cnemidophorus*, *Crocodilurus*, *Dicrodon*, *Dracaena*, *Kentropyx*, *Teius* and *Tupinambis*. The smaller species, first termed 'microteiids' by Ruibal (1952), made up Groups II, III and IV, and were distinguished by head scale patterns and digit morphology (Group II), and body elongation with loss or reduction of limb and girdle elements and external ear openings (Groups III and IV) (Boulenger, 1885). This arrangement formed the basis for many subsequent systematic treatments of the group (e.g. Cope, 1900; Burt & Burt, 1931; Ruibal, 1952; MacLean, 1974; Presch, 1974, 1980, 1983). The recognition of two formal taxonomic categories of teiids, Teiinae (Boulenger's Group I) and Gymnophthalminae (Boulenger's Groups II, III and IV), was first proposed by MacLean (1974), and then independently by Presch (1974). Recognition of the gymnophthalmines as a separate family, the Gymnophthalmidae, was proposed independently by Presch (1983) and Estes (1983), and has been followed in most recent systematic treatments of

Squamata (Estes *et al*., 1988; Schwenk, 1988; Evans & Barbadillo, 1997, 1998; Evans & Chure, 1998; Lee, 1998; Caldwell, 1999).

Owing to a general paucity of material, there have been few detailed studies of gymnophthalmid anatomy and systematics, and most systematic studies are restricted to revisions of genera. Many of these relied exclusively on external morphology (e.g. Uzzell, 1959, 1966; Dixon, 1973, 1974a; Montanucci, 1973), but karyotype data (Gorman, 1970) and internal anatomical features including hemipenial morphology (Uzzell, 1965, 1969, 1970, 1973; Uzzell & Barry, 1971; Böhme, 1988; Kizirian, 1996) and tongue morphology (Uzzell, 1969; Harris, 1985; Schwenk, 1988) were included in some analyses.

The literature on gymnophthalmid cranial osteology is extremely limited. The earliest report of any aspect of cranial osteology is that of Sinitsin (1928), who provided a brief discussion of the differences in the anterior portions of the skull of teiids and gymnophthalmids. He illustrated differences in the relative contributions of the premaxilla and nasals to the border of the nares, as well as differences in relative position and architecture of the septomaxillae with respect to the nasal cavity and vomeronasal organ. MacLean (1974) included discussion of cranial osteology in his analysis of gymnophthalmid feeding mechanisms. His illustrations of the skull and jaws of *Gymnophthalmus speciosus*, *Alopoglossus buckleyi*, *Proctoporus unicolor* and *Bachia bresslaui* are among the few published figures of complete gymnophthalmid skulls, the only others being those of *Iphisa elegans* (Dixon, 1974b) and of *Pantodactylus schreibersii* (López & Cabrera, 1995). The latter study included both a skull description and a commentary on the structure of the palate and dentition in other gymnophthalmids. Estes (1983) listed osteological characters for Gymnophthalmidae, but many of these were subsequently shown to be variable (Estes *et al*., 1988). This later work provided a list of 12 putative gymnophthalmid synapomorphies, including five derived from the skull, and three from the hyoid skeleton. Finally, two published in-group phylogenies for Gymnophthalmidae (Presch, 1980; Hoyos, 1998) utilized cranial characters to help determine relationships; both papers provide drawings of parts of the skull and mandible to illustrate character states in various species.

Apart from these major studies, a few isolated reports include information on gymnophthalmid cranial anatomy. These include a sketch of the skull of *Bachia trisanale* (Presch, 1975); illustrations of the hyoid skeleton of *Neusticurus rudis* and *Tretioscincus bifasciatus* (Beebe, 1945); a brief discussion and illustration of the hyoid skeleton in *Neusticurus bicarinatus* (Richter, 1933); and illustrations of the hyoid, mandible and articulated skull of *Iphisa elegans* (Dixon, 1974b). Dixon (1973) recorded the presence of simple, conical teeth in *Bachia* and of tricuspid teeth in *Heterodactylus*; subsequently he reported simple conical teeth in *Anotosaura* as well (Dixon, 1974a). Olson, Marx & Rome (1986) provided a brief description of the dentition of *Gymnophthalmus sumichrasti* (= *G. speciosus*; Peters & Donoso-Barros, 1986), and some aspects of the dental morphology of four species of *Proctoporus* (*P. hypostictus*, *P. occulatus*, *P. simoterus* and *P. unicolor*) can be seen in the figures provided by Kizirian (1996). Montanucci (1973) reported individual variation in the relative positions of cranial elements in *Pholidobolus* but found no consistent characters to differentiate species.

The current tentative understanding of gymnophthalmid phylogeny (Presch, 1980; Kizirian, 1994; Hoyos, 1998; Pellegrino *et al*., 2001) is due at least in part to an inadequate understanding of the morphology of this diverse group. In this paper, we present a detailed description of the skull and associated hyoid skeleton of one species of *Neusticurus*, a genus widely distributed in South America, with 11 currently recognized species. Relationships among these species are not well understood, and recent analyses (Kizirian, 1994; Pellegrino *et al*., 2001) failed to recover a monophyletic *Neusticurus*.

We document the basic structure of the skull of *Neusticurus ecpleopus*, note the range of observed variation in the expression of various morphological features and include comments on postnatal cranial ossification, based on a series of dry skeletal preparations and cleared and stained specimens. Our goals are to provide a detailed description of the cranial osteology of a single species, document the level of variation, and thus establish a baseline for further morphological and systematic analyses of gymnophthalmids. We also provide preliminary comparisons of the skull of *N. ecpleopus* with that of teiids and other gymnophthalmids.

Neusticurus ecpleopus is a relatively small, diurnal species (Uzzell, 1966; Vitt & de la Torre, 1996) found in southern Colombia, Ecuador, Peru, north-western Bolivia and northern Brazil (Uzzell, 1966; Vanzolini, 1972; da Cunha, Nascimento & Sàuer de Ávila-Pires, 1985; Avila-Pires, 1995). These lizards are active foragers, and their diet includes earthworms and a diverse assemblage of insects (da Rocha, 1991; Vitt & de la Torre, 1996). From what is known of its natural history, *N. ecpleopus* is a forest-dwelling species that is generally found close to water, especially small streams, pools and swamps, in relatively shaded habitats (Uzzell, 1966; Fitch, 1968; Vanzolini, 1972; Dixon & Soini, 1975; Sherbrooke, 1975; da Rocha, 1991; Vitt & de la Torre, 1996) and at elevations ranging from

1500 m to below 50 m (Uzzell, 1966; Dixon & Soini, 1975).

MATERIAL AND METHODS

Specimens of *Neusticurus* examined are shown in Appendix 1. The study series included 11 dry skulls ranging in size from juvenile to adult, and 22 cleared and double-stained specimens prepared by one of us (J.A.M.) following a modified version of the protocol of Pothoff (1984). Specimens in the latter series range from 22.4 to 63.2 mm snout–vent length (SVL), with skull lengths varying from 8 to 16 mm. Hatchling size for *Neusticurus ecpleopus* in Peru averages 21.5 mm SVL, with females reaching sexual maturity at 53 mm SVL and maximum size at 62 mm SVL, and males reaching sexual maturity at 52 mm SVL and maximum size at 72 mm SVL (Sherbrooke, 1975; a slightly larger male was reported from Bolivia by Uzzell, 1966).

One of the dry skulls (MCZ 163394) was disarticulated (most but not all elements are present), and this permitted examination of internal structures and sutures. Its frontal is equivalent in size to that of a skull approximately 12 mm in length (MVZ 163389).

This represents an immature individual at about 67% adult size (SVL approximately 45 mm). This immaturity must be taken into account in the descriptions that follow, although ontogenetic variation is discussed as appropriate.

INSTITUTIONAL ABBREVIATIONS

CAS, California Academy of Sciences, San Francisco; CJB, Christopher J. Bell skeletal collection, Austin, Texas; KU, University of Kansas Museum of Natural History; NAUQSP-JIM, Northern Arizona University Quaternary Sciences Program, Jim I. Mead collection, Flagstaff; MCZ, Museum of Comparative Zoology, Harvard; MVZ, Museum of Vertebrate Zoology, The University of California at Berkeley; USNM, National Museum of Natural History, Washington, DC.

THE SKULL OF *NEUSTICURUS ECPLEOPUS*

GENERAL FEATURES (FIGS 1–3)

The skull of *Neusticurus ecpleopus* is small (range of dry skull length of specimens used in this analysis: 11.7–16 mm; Appendix 1), with large orbits and a small, sharply pointed rostrum (Fig. 1A,B). The upper
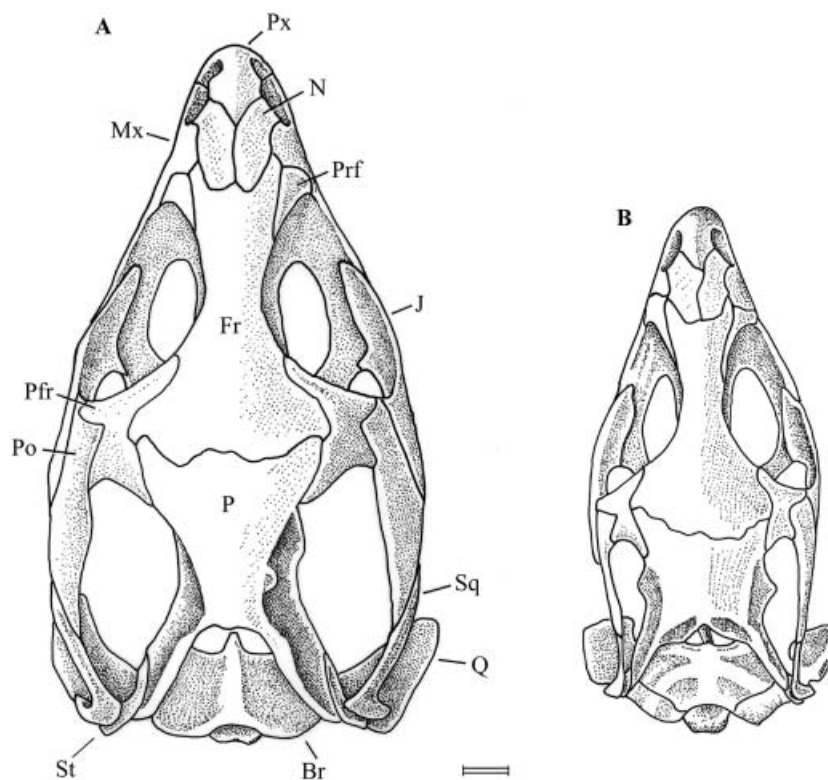
Figure 1. Dorsal views of the skull of *Neusticurus ecpleopus*; A, adult (MVZ 163410) and B, juvenile (MVZ 163397). Abbreviations: Br, braincase; Fr, frontal; J, jugal; Mx, maxilla; N, nasal; P, parietal; Pfr, postfrontal; Po, postorbital; Prf, prefrontal; Px, premaxilla; Q, quadrate; Sq, squamosal; St, supratemporal. Scale bar = 1 mm.
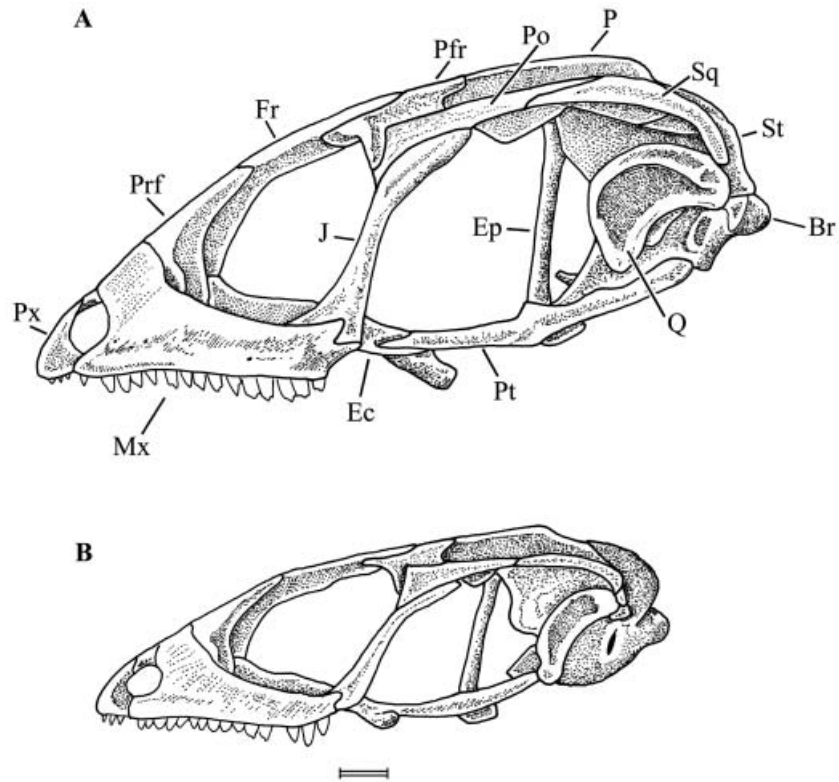
Figure 2. Left lateral views of the skull of *N. ecpleopus*; A, adult (MVZ 163410) and B, juvenile (MVZ 163397). Abbreviations: as in Figure 1, with Ec, ectopterygoid; Ep, epipterygoid; Pt, pterygoid. Scale bar = 1 mm.

temporal fenestrae are open, although slightly narrowed, and both postorbital and supratemporal bars are complete (Fig. 2A,B). Posteriorly, all but the lateral edges of the supraoccipital are fully exposed behind the parietal and, as in many small lizards, the braincase is relatively large, with conspicuous semicircular canals. The bones of the skull roof are robust, those of the palate more gracile. In the palate (Fig. 3A,B), the suborbital and subtemporal fenestrae are large, whereas the interpterygoid vacuity is narrow, reaching only to the midpoint of the palatines. There is an extended primary palate (Fig. 3C).

of the trigeminal nerve (Vi; Oelrich, 1956). The alveolar border has positions for 11 small, unicuspid teeth, arranged with five on either side of a median tooth. Above them is a narrow palatal shelf that appears strongly V-shaped (apex anterior) in ventral view. The posterolateral extremities of the shelf bear small facets for the anterolateral processes of the maxillae. Medially, in the central part of the bone, the edges of the shelves are deflected ventrally and carry dorsomedial facets for the anteromedial processes of the maxillae. By this arrangement, the premaxilla and maxillae are firmly interlocked.

PREMAXILLA

The premaxilla is a small, robust, unpaired element forming the anterior tip of the snout. The bones are already fused at hatching and have the adult shape. The dorsal (nasal) process is broad and flares distally, but then ends in a tapered tip. Ventrally, the process bears paired nasal facets separated by a low ridge. At its junction with the alveolar portion, the base is pierced by a pair of short, nearly vertical canals that exit anteroventrally via foramina. In other lizards these canals carry branches of the ophthalmic division

MAXILLA

The maxilla is triradiate, with anterior, dorsal (facial), and orbital processes, and a strong medial shelf (Fig. 4A). The anterior premaxillary process is bifurcate, with a strong anteromedial process and a shorter anterolateral process meeting the premaxilla as described above. The facial process is anteroposteriorly rather short and relatively tall; it meets the nasal dorsally and the prefrontal medially and posteriorly. Seen in dorsal view, it is angled medially. The long orbital process tapers gradually
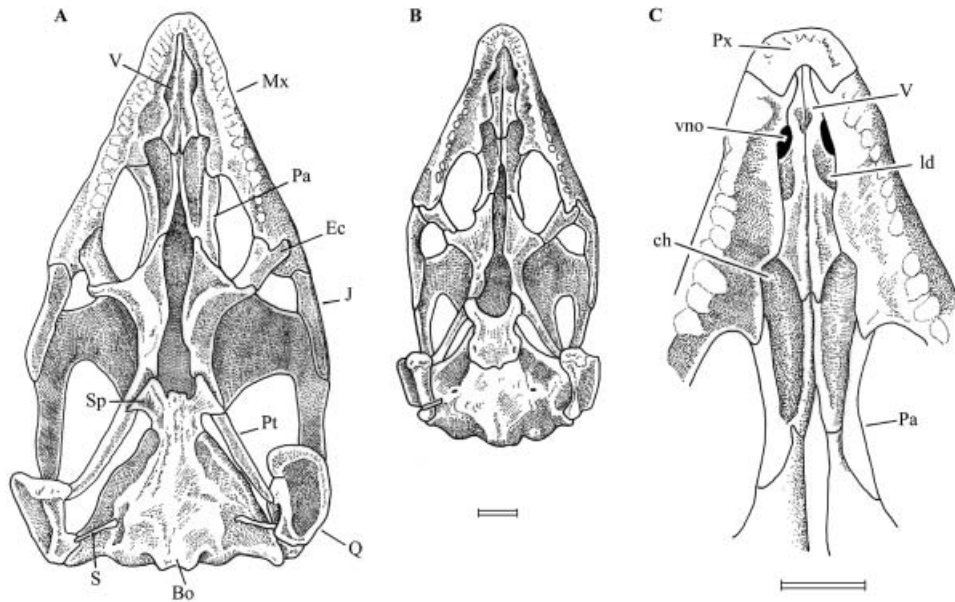
Figure 3. Palatal views of *N. ecpleopus*; A, adult (MVZ 163410); B, juvenile (MVZ 163397); and C, enlargement of the anterior palatal region in MVZ 163397. Abbreviations: Bo, basioccipital; Ec, ectopterygoid; J, jugal; ld, opening of the lacrimal duct; Mx, maxilla; Pa, palatine; Pt, pterygoid; Px, premaxilla; Q, quadrate; Sp, sphenoid; St, stapes; V, vomer; vno, opening of vomeronasal organ. Scale bars = 1 mm.
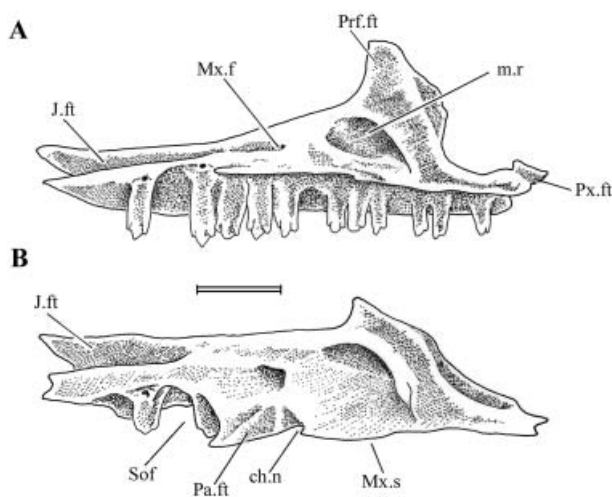
Figure 4. *Neusticurus ecpleopus*. Left maxilla (MVZ 163394) in: A, medial and B, dorsomedial views. Abbreviations: ch.n, choanal notch; J.ft, Jugal facet; m.r, medial recess for nasal sac; mx.f, maxillary foramen; mx.s, maxillary shelf; Pa.ft, palatine facet; Prf.ft, prefrontal facet; Px.ft, premaxillary facet; sof, embayment for suborbital fenestra. Scale bar = 1 mm.

towards the rear, but ends in a bifurcated tip that interlocks with the jugal (Fig. 4B). Laterally, the alveolar margin is marked by a line of small nutrient foramina. The alveolar border itself bears 15–18

tooth positions, depending on the size/age of the individual.

Above the tooth row, the maxillary shelf varies in its width and regularity, the differences relating to the structure of the choanal region medial to it. Anteriorly, the shelf is quite narrow, corresponding to the position of the anterior opening for the vomeronasal organ. The shelf then expands, reaching its maximum width about two-thirds of the way along the bone. In this region, the shelf is juxtaposed against the vomer to close the choanal groove. Further posteriorly, the shelf is notched, the notch corresponding to the anterolateral margin of the choana (Fig. 4B). Just behind this point, the shelf is sharply emarginated, the resulting embayment forming the anterior margin of the suborbital fenestra.

The dorsal surface of the shelf is marked by both foramina and facets. A large foramen pierces its widest part, carrying the maxillary division of the trigeminal nerve (Vii) and accompanying blood vessels into the superior alveolar canal. The deepest and most clearly demarcated facet is that at the posterior end of the orbital process for the jugal. Immediately medial to this is a smaller shelf facet for the lateral head of the ectopterygoid. Further forward, the widest part of the shelf bears a small medial facet for the palatine. The descending process of the prefrontal also contacts the maxillary shelf but it leaves no obvious facet on the maxilla. The medial surface of the facial process is

smooth anteriorly, but bears a large posterior overlap facet for the prefrontal. Below this, a sharp, almost horizontal crest crosses the bone (Fig. 4A). Ventrally, this crest borders a deep excavation that houses a large, blind ending lateral extension of the nasal sac (Stebbins, 1948), a feature of teiioid and lacertid lizards (C. J. Bell & S. E. Evans, pers. observ.). The rear of the bone is bifurcated and clasps the ventrolateral aspect of the jugal.

NASAL

The nasal is a small ellipsoid bone that meets the premaxilla anteriorly via a dorsal shelf facet, and the frontal posteriorly (ventral shelf facet). The anterior one-third of the bone is overlapped by the premaxilla, and the posterior one-third overlaps the frontal. The nasals are partially separated anteriorly and posteriorly by the premaxilla and frontal, respectively. Lateral frontal ridges separate the nasals from the prefrontals.

FRONTAL (FIG. 5A–C)

In the smallest specimen examined (KU 48246), the frontals are already fused and the compound bone is strongly built. The frontal is hourglass shaped. Its posterior margin, still slightly concave in the hatchling (Fig. 5A), is two to three times the anterior width in the adult (Figs 5B, 6A,B), and there is a strong constriction between the orbits. In all except the largest

specimen (MVZ 163410), where there is a slight ornamentation, the dorsal surface lacks sculpture. The anterodorsal border bears small, paired shelf facets for the nasals, separated medially by a low ridge and flanked laterally by further ridges (Fig. 5A). Thus, the anterior margin of the frontal appears triradiate in the articulated skull (Fig. 1A,B). The frontoparietal margin is more complex and appears sinuous or W-shaped. Paired lateral tabs, already weakly developed in the hatchling, overlap the anterolateral surface of the parietal, whereas paired rounded extensions overlie the parietal medially upon the ontogenetic closure of the parietal fontanelle (Figs 5A, 6B). This arrangement contributes to the formation of a firm, interlocking suture (see below).

In ventral view (Fig. 5B), the anterior edge of the bone appears straight. The cristae cranii (subolfactory processes, orbital ridges) are strongly developed and meet anteriorly to form a tubular structure that encloses the olfactory tracts and strengthens the bone in cross-section. This arrangement is already present at hatching. Anteroventrally, the tips of the cristae extend into orbitonasal flanges that buttress the prefrontals medially and contact the dorsomedial surfaces of the palatines (Fig. 5C). Posteriorly, the cristae diverge, ending in tips (paired lateral tabs) that overlie the parietal. Medial to this, each side bears a shelf facet that accommodates the anteromedial process of the parietal. The frontal and parietal thus intercalate to form a strong
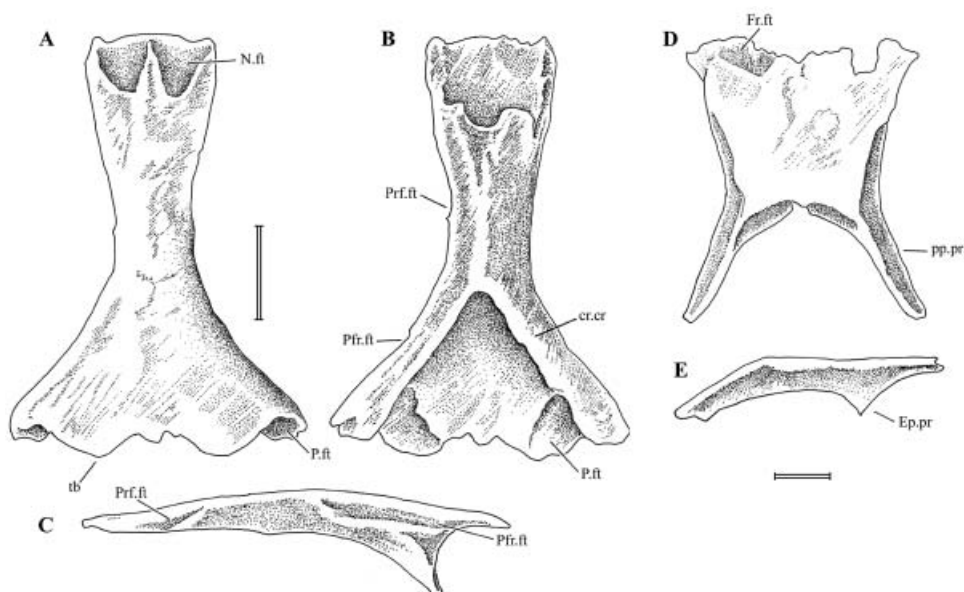
Figure 5. *Neusticurus ecpleopus*. A–C, frontal (MVZ 163394) in A, dorsal; B, ventral; and C, left lateral views; D,E, parietal (MVZ 163394, with slight damage to right side) in D, dorsal view; E, right lateral view. Abbreviations: cr.cr, crista cranii; Ep.pr, epipterygoid process; Fr.ft, frontal facet; N.ft, nasal facet; P.ft, parietal facet; Pfr.ft, postfrontal facet; Prf.ft, prefrontal facet; pp.pr, postparietal process; tb, frontal tab. Scale bar = 1 mm.
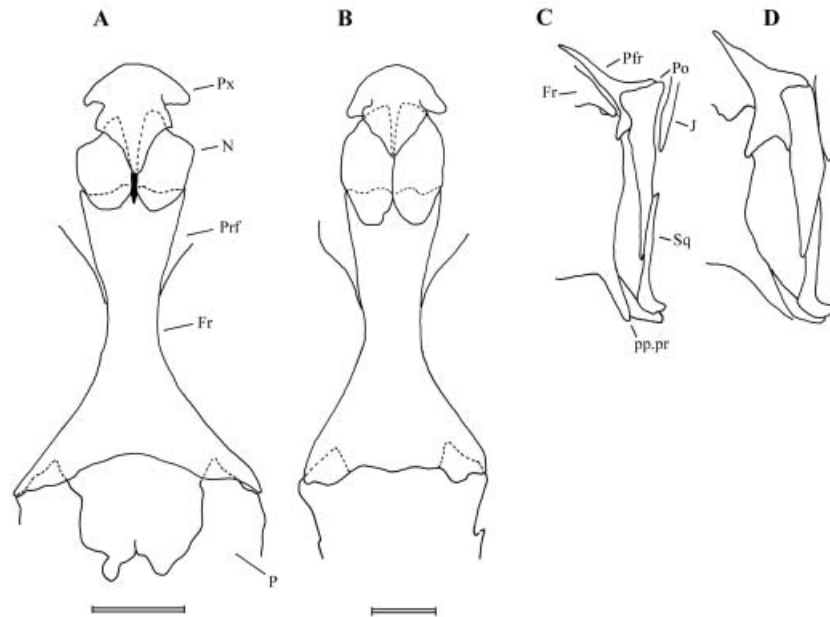
Figure 6. Development of the skull roof in *Neusticurus ecpleopus*; A,C, hatchling, 22.4 mm SVL (KU 148246); B,D, adult, 59.1 mm SVL (MVZ 163202). A,B, dorsal views of anterior skull roof; C,D dorsal views of the postorbital region. Abbreviations as in Figure 1, with pp.pr, postparietal process of parietal. Scale bars = 1 mm, with C and D at the same scales as A and B, respectively.

sinuous suture that would appear to preclude mesokinetic bending.

Seen in lateral view (Fig. 5C), the posterior part of the frontal is very shallow, and bears a weak facet for the anterior limb of the postfrontal. The bone deepens anteriorly and carries strong, but shallow, facets for the orbital processes of the prefrontals.

PARIETAL

The parietal forms a flattened, slightly sculptured table that is wider anteriorly than posteriorly, and has sloping lateral margins (Fig. 5D,E). At no point in its post-hatchling development is there a trace of either a midline suture or a parietal foramen. The adductor muscles are confined to the near-vertical lateral margins, neither invading the dorsal surface of the skull nor extending ventrally. The postparietal processes are nearly horizontal with very little ventral deflection, and are divergent. They are widest at their bases, tapering posteriorly and triangular in cross-section, with a dorsal ridge running the length of the process. This ridge separates a small medial shelf for the nuchal muscles (spinalis capitis, rectus) from the lateral surface for adductor muscles; it becomes more pronounced with age/size.

The anterior margin of the parietal is wide, with thin anteromedial tabs that run below the frontal and small lateral recesses that accommodate the frontal tabs. The ventral surface bears paired medial excavations for the brain, flanked laterally by low descending crests that are developed further posteriorly into small descending epipterygoid processes (Fig. 5E). These have narrow bases. Posteromedially, the pit for the processus ascendens of the supraoccipital lies mostly in the posterior surface of the bone, notching the ventral aspect only slightly.

Parietal shape changes markedly with age/size (Fig. 6C,D). The prominent parietal fontanelle present in the hatchling closes by roughly 77% maximum size. The parietal table, nearly square initially, becomes longer and more tapered posteriorly. The postparietal processes, barely reaching the supraoccipital/opisthotic suture in the hatchling (Fig. 6C), extend well beyond it in the adult (Fig. 6D), becoming more deeply crested in the process. In the largest individuals, the midpoint of the lateral parietal margin may be drawn out laterally, forming a small thinly ossified process (e.g. on the right side of MVZ 163410).

PREFRONTAL (FIG. 7G,H)

This is a relatively gracile bone in *Neusticurus ecpleopus*. It can be divided into a broad, medially concave body that meets the maxilla and contributes to the anterior margin of the orbit, and a slender posterodorsal orbital process that contacts the frontal (Fig. 7G). The main body of the bone is flattened laterally and
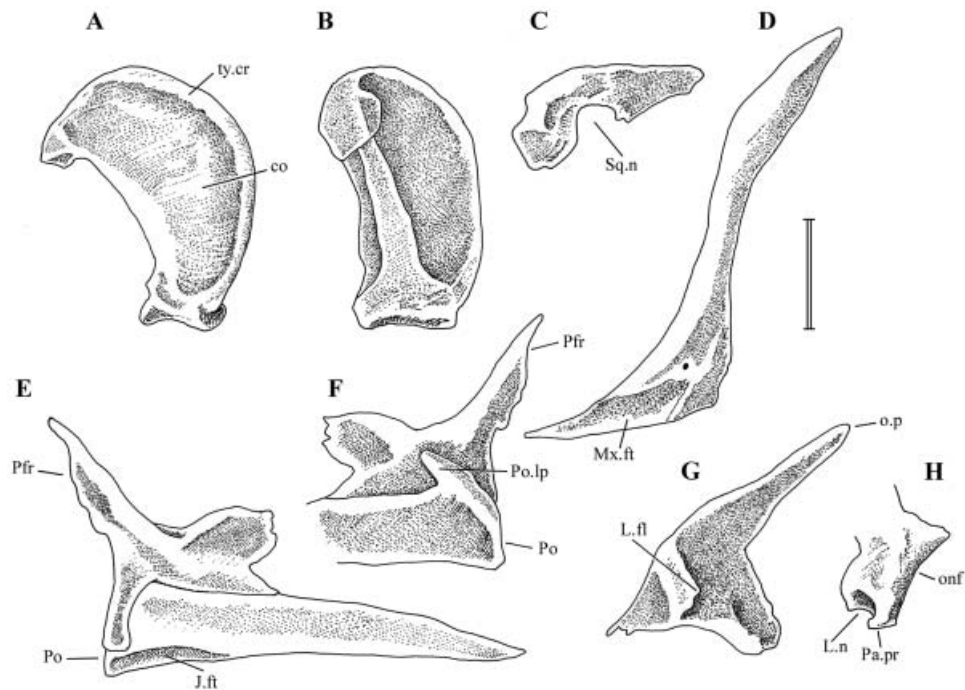
Figure 7. *Neusticurus ecpleopus*. Cranial elements (MVZ 163394); A–C, right quadrate, in A, lateral view; B, posterior view; C, dorsal view; D, left jugal, lateral view; E, left postfrontal + postorbital, lateral view; F, partial medial view of elements from E; G,H, left prefrontal in G, lateral and H, partial posterior views. Abbreviations: co, conch; J.ft, jugal facet; l.fl, lacrimal flange; l.n, lacrimal notch; mx.ft, maxillary facet; onf, border of orbitonasal foramen; Pa.pr, palatine process; Pfr, postfrontal; Po, postorbital; Po.lp, postorbital lappet; Sq.n, squamosal notch; ty.cr, tympanic crest. Scale bar = 1 mm.

bears a large anterior facet for the maxilla. The posterior margin curves medially and contributes to the orbitonasal flange. Ventrally, the orbital rim is extended into a small process that meets the medial shelf of the maxilla, as well as a small posterolateral lappet (lacrimal flange) that curves out above the lacrimal foramen (Fig. 7H). There is no free lacrimal bone in our dry skulls, and the lacrimal foramen lies between the prefrontal and the maxilla. However, in the smallest of the cleared and stained specimens (KU 48246), the orbital margin of the right prefrontal is overlain by a sliver of bone that is already partially fused in place. It lies in the position of the lacrimal flange, suggesting that this region of the adult bone may be compound.

POSTFRONTAL (FIG. 7E,F)

The postorbital and postfrontal are separate but closely associated; they appear to form a functional unit. The postfrontal is quadriradiate (Fig. 6D), although its posterior portion is only weakly bifid in the hatchling (Fig. 6C). Its anteromedial and posteromedial processes embrace the frontoparietal suture, fitting against very shallow surfaces on those bones. This fit becomes tighter with increasing age/size. The

orbital margin is slightly thickened, but lacks the deep flanges seen in some lizards (e.g. many iguanians, some large teiids). The anteromedial process is longest; the anterolateral process is shorter and extends down the orbital margin of the postorbital, limiting the latter to a small orbital contribution (Fig. 7E). The ventral margin of the bone sits in a narrow groove in the dorsal margin of the postorbital and is drawn posteriorly into a small spur that borders the anterior apex of the supratemporal fenestra (Fig. 7E,F).

POSTORBITAL (FIG. 7E,F)

The postorbital is a long narrow bone that meets the jugal in a weak anteroventral articulation and tapers posteriorly to its junction with the squamosal (Fig. 7E). In lateral view, it appears to have an elongate abutting articulation with the more dorsal postfrontal, but in medial view is seen to extend a small tongue-like process that braces the postfrontal (Fig. 7F).

JUGAL (FIG. 7D)

This is a sigmoid bone with a broad ventral foot and a more slender dorsal postorbital process (Fig. 7D). The

ventral foot is widest posteriorly, tapering anteriorly where it inserts into the facet in the orbital process of the maxilla. The ventrolateral surface bears two adjoining facets, a large dorsal one for the maxilla, and a smaller medial one for the ectopterygoid. The postorbital process is rounded in cross-section but becomes more flattened dorsally where the jugal lies against the ventral margin of the postorbital.

SQUAMOSAL

The squamosal has the hockey-stick shape of most scleroglossan lizards, and lacks the dorsal process of many teiids (Estes *et al*., 1988). The tapering anterior region, which extends progressively further forward in ontogeny, meets the postorbital (Fig. 6C,D); in some specimens (e.g. MVZ 163399, 174957) it may closely approach, but does not contact, the jugal. The ventrally recurved posterior part abuts the supratemporal. Its ventral tip, the squamosal peg, meets the tympanic crest of the quadrate, but there is some variation in its relationship to the quadrate notch. Hoyos (1998) used this relationship as a character (peg in vs. behind the notch), and coded *Neusticurus* as having the peg lying behind the notch in the tympanic crest. However, in the majority of specimens examined (both skeletal and cleared/stained), the squamosal peg lies within the quadrate notch. Only two specimens, one juvenile (MVZ 163395) and one adult (MVZ 163399), have the squamosal peg lying behind the quadrate notch. It seems most likely that this condition is an artefact of preservation.

SUPRATEMPORAL

The supratemporal is unusual in being recessed along most of its length. The resulting trough-like bone wraps around the posterior two-thirds of the postparietal process of the parietal, emerging on its ventrolateral and ventromedial surfaces. Posterior to that articulation, the supratemporal curves ventrally, running medial to the squamosal to meet the cephalic condyle of the quadrate and the paroccipital process of the otooccipital.

EPIPTERYGOID

This is a long, slender bone of relatively constant diameter, spanning the gap between the pterygoid and the skull roof (Fig. 2A,B). Ventrally, its base rests in the fossa columellae of the pterygoid. Dorsally, it fits between the tip of the epipterygoid process of the parietal and the tip of the alar process of the prootic lying immediately behind it. This relationship remains constant from hatchling to adult, although the primary contact is initially with the parietal.

QUADRATE (FIG. 7A–C)

This is a relatively small but very robust bone. The lateral conch is well defined but two dimensional and has a relatively weak tympanic crest, even in fully grown individuals. The posterior margin is buttressed by a strong column of bone that ends ventrally in a narrow, concave mandibular condyle (Fig. 7B). The dorsal margin of the tympanic crest is notched for the squamosal peg (Fig. 7C), and then expands slightly into a curved cephalic condyle that meets the supratemporal and paroccipital processes. This dorsal region of the quadrate is cartilaginous in the hatchling, ossifying progressively up from the body of the quadrate and then down into the tympanic crest. It is fully ossified by about 95% maximum size (MVZ 163202). The narrow medial wing of the quadrate expands ventrally into a small pterygoid lappet.

VOMER

The vomers are slender, needle-like bones, partially fused in their midsection. They taper anteriorly towards the premaxilla, but meet the maxillary shelf laterally. The combined bones expand gradually posteriorly, but end by tapering again into their contact with the palatines. Here they are separated slightly by the medial ridge of the palatines. Their palatal surface is otherwise fairly featureless. Their dorsal surface is divided into anterior vomeronasal and posterior nasal regions by a transverse flange. Just anterior to the flange, the lateral margin of the bone is emarginated by paired notches. These are separated by a very slender anterolateral process that meets the maxillary shelf to create anterior and posterior foramina. According to Oelrich (1956), based on the iguanian *Ctenosaura*, the anterior foramen is for the vomeronasal duct, and the posterior one is for the lacrimal duct.

SEPTOMAXILLA

The septomaxilla is a curved sheet of bone, concave medially, convex laterally, with a rounded anterodorsal margin. It is orientated obliquely medial to the external nares so that the vomeronasal apparatus lies ventral and medial to it, whereas the nasal apparatus lies dorsal and lateral (Sinitsin, 1928). A small lateral process abuts the anterior margin of the maxilla, and its inferior rim rests on the maxillary shelf.

PALATINE

The palatine is a lightly built bone, widest anteriorly and tapering posteriorly where it meets the pterygoid
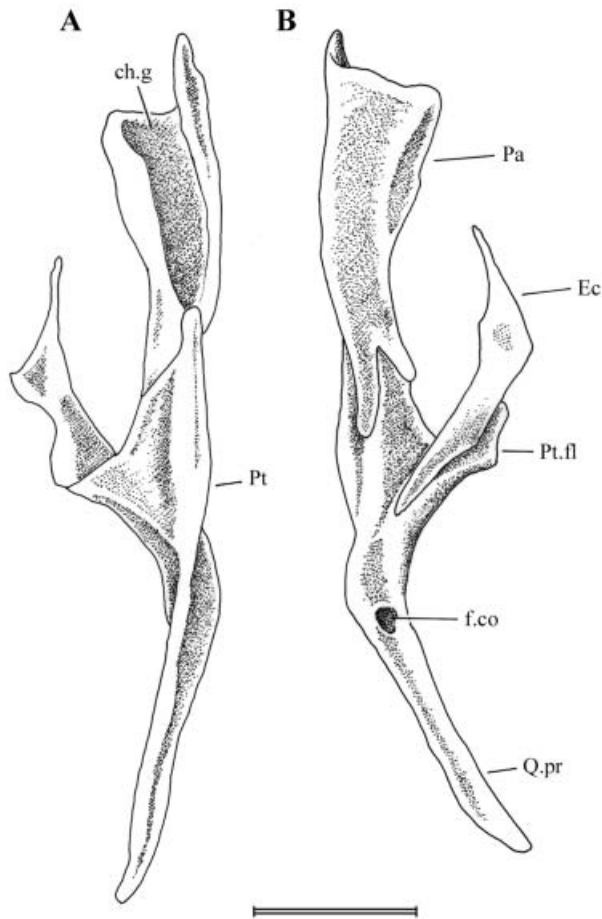
Figure 8. *Neusticurus ecpleopus*. Palatine, pterygoid and ectopterygoid in A, palatal and B, dorsal views. Abbreviations: ch.g, choanal groove; Ec, ectopterygoid; f.co, fossa columellae; Pa, palatine; Pt, pterygoid; Pt.fl, pterygoid flange; Q.pr, quadrate process. Scale bar = 1 mm.

(Fig. 8A,B). The dorsal surface is fairly featureless, whereas the ventral surface is deeply grooved in an anterolateral to posteromedial direction, with the groove flanked medially by a strong ridge (Fig. 8A). This deep groove runs from the choanal opening and carries the choanal duct back towards the midline. In palatal view (Fig. 8A), the palatine seems simply to taper posterolaterally, but the dorsal view (Fig. 8B) reveals a tongue-in-groove joint whereby a palatine tongue fits into a socket on the dorsal surface of the pterygoid. Anterolaterally, the palatal surface bears a small ventrolateral shelf that overlaps the maxillary shelf, and the vertical medial edge of the bone carries a slender facet for the vomer. The anterior end of the bone is angled dorsally and contacts the descending process (crista cranii) of the frontal, deepening the anterior part of the choana and forming a firm orbitonasal flange.

PTERYGOID (FIG. 8A,B)

The pterygoid is a slender, gracile bone by comparison with the robust build of the skull roof. It consists of a tapering anterior plate that meets the palatine as described above then curves posterolaterally into a small pterygoid flange (Fig. 8A,B). The tip of this flange is deflected anterolaterally into a pointed process that slots into the medial aspect of the ectopterygoid. Seen dorsally (Fig. 8B), a narrow medial spur of the ectopterygoid extends along the anterior margin of the pterygoid flange. The pterygoid tapers posteriorly into a long and very slender quadrate process that has a narrow, pointed tip. The ventromedial surface of this process is planar. Lacking a discrete basipterygoid fossa, it more closely resembles the condition in teiids, except that the surface is less convex. The dorsal fossa columellae is ovoid and fully open, with a short trough or excavation extending a short distance posterior to it.

ECTOPTERYGOID

The ectopterygoid runs from posteromedial to anterolateral, but its primary axis is anterior. The lateral head contacts both the maxilla and the jugal, but the facet is very shallow and this articulation is not strong. The medial portion of the bone is elongated, slotting dorsally into the pterygoid flange. There is very little depth to the flange as constructed, even in fully grown adults. This is in striking contrast to the condition in some lizard taxa (e.g. many iguanians), where the pterygoid/ectopterygoid flange is deep and acts to guide movements of the lower jaw.

GENERAL FEATURES OF THE BRAINCASE

In dorsal view, most of the braincase lies fully exposed behind the parietal (Fig. 1A,B). As is common in diminutive lizard species, the semicircular canals are large and prominent, their paths being clearly visible in the adult.

In the hatchling, all elements of the braincase are unfused except the exoccipital and opisthotic; this compound bone is here termed the otooccipital. Between the sphenoid and the basioccipital lies a narrow basicranial fenestra, but the remaining bones are separated only by narrow zones of cartilage. The elements of the basal plate begin to fuse at their lateral margins at 35% maximum size (KU 109803). They are followed by the otooccipital and basioccipital as early as 40% maximum size (MVZ 174949), then the supraoccipital and otooccipital and the prootic and sphenoid at 46% maximum size (MVZ 175920). The basicranial fenestra is closed by 63% maximum size (MVZ 174953). The prootic and otooccipital begin to fuse at 77% maximum size (MVZ 174896), and by 95%

maximum size (MVZ 163202), fusion of the basicranium is complete.

ORBITOSPHENOID

These are seen in cleared and stained material spanning the post-hatchling size range, but are lost in available dry skeletal preparations. Compared with those of other taxa, the orbitosphenoids are very slender. They appear to bifurcate dorsally, with long, slender ventral processes.

SPHENOID

The sphenoid is small and narrow relative to the large basioccipital. The basipterygoid processes are more anteriorly than laterally directed, and are distally flared in the adult (Fig. 3A). The tips of the basipterygoid processes are rather flattened dorsoventrally, like those of teiids, but they lack the distal teiid concavity, so that the tip lies against the planar surface of the pterygoid rather than wrapping around it (Evans, in press). Between the processes is a very slender parasphenoid rostrum. The sphenoccipital suture, where visible, is straight and short, with no lateral parasphenoid wings (Fig. 3B). The openings of the vidian canals lie a short distance behind the base of the basipterygoid process, fully within the sphenoid rather than on or close to the prootic–sphenoid suture as in many lizards. The anterior opening of the canal lies ventrolateral to the hypophysial fossa, which is unusual in being very shallow. At its greatest dorsal extent, the ala basisphenoidei contributes to the inferior border of the incisura prootica. Below this, the base of each basipterygoid process is grooved by the lateral head vein. There is no overhanging vidian bridge, but anteriorly the groove is floored by a small crest. Foramina for the internal carotid artery are present, but there is virtually no development of a dorsum sellae – just a shallow ridge, the lateral edges of which are penetrated by short abducens canals that transmit cranial nerve VI. This unusual low dorsum sellae is a feature of most gymnophthalmid taxa, the dorsal region remaining unossified and represented by a sheet of connective tissue.
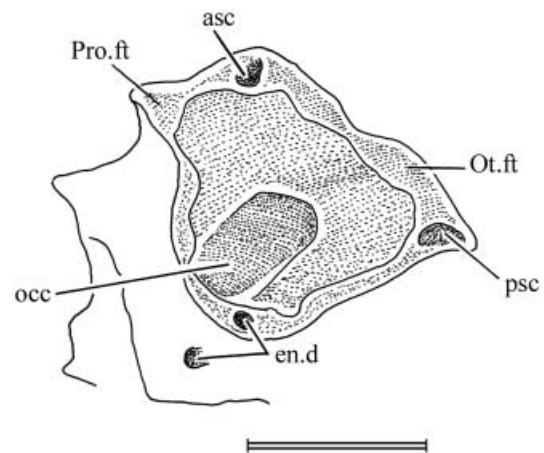
BASIOCCIPITAL

The basioccipital is a relatively simple pentaradiate structure. The posterior apex contributes to the occipital condyle, and the sphenoccipital suture has a small midline notch. The ventral surface of the basioccipital is smooth and convex, except posterolaterally, where it is drawn out into shallow basal tubera, the size of which increase with age/size. In individuals that are about one-half maximum size, apophyseal ossifications develop on the tips of the tubera. These begin to fuse at around 70% maximum size, and are no longer discernible as separate ossifications by about 80% maximum size. The narrow lateral margins of the basioccipital are divided into an exoccipital (otooccipital) facet posteriorly and a prootic facet anteriorly. These facets are separated by a small notch, leading into a shallow groove that represents part of the floor of the recessus scalae tympani. The participation of the bone in the margin of the lateral (and, to a lesser extent, the medial) opening of the recessus scalae tympani is restricted by a contact between the exoccipital and opisthotic portions of the otooccipital.

SUPRAOCCIPITAL

The supraoccipital is anteroposteriorly short but wide. Its dorsal midline gives rise to a short processus ascendens, from which arises the ascending process of the tectum synoticum, extending into a small pit on the ventral surface of the parietal, just anterior to the posteroventral margin of that bone. The supraoccipital is flattened dorsally (no midline crest), and the courses of the anterior and posterior semicircular canals are clearly visible, converging onto the anteromedial region of the bone where they form the osseous common crus. Ventrally, the paired supraoccipital components of the otic capsule are large and separated by only a narrow cranial roof. The internal surface is smooth except for the common opening of the osseous common crus on the medial wall. Seen from the cranial surface (Fig. 9), there is also a small foramen for the endolymphatic duct, but it does not

Figure 9. *Neusticurus ecpleopus*. Ventrolateral view of left capsular region of supraoccipital (MVZ 163394). Abbreviations: asc, path of anterior semicircular canal; en.d, canal for the endolymphatic duct; occ, osseous common crus; Ot.ft, otooccipital facet; psc, path of posterior semicircular canal; Pro.ft, prootic facet. Scale bar = 1 mm.

open from the capsular surface of the supraoccipital. Rather, it exits from a small canal that perforates the prootic facet, and clearly opened from that bone. Anterolaterally, the canal for the anterior semicircular duct pierces the prootic facet on route to the osseous common crus.

PROOTIC (FIG. 10A–C)

The prootic provides the anterior component of the otic capsule and contributes to the wall of the braincase. For description, the bone can be divided into anterior cranial and posterior otic parts, but there are three distinct surfaces – lateral, anteromedial and posteromedial. The posteromedial surface forms the interior of the otic capsule. Anteriorly, the prootic frames a C-shaped opening, the incisura prootica, for the exit of the trigeminal nerve (Fig. 10A,B). Posterolaterally, a smaller C-shaped notch marks the prootic contribution to the fenestra ovalis (Fig. 10A).

The lateral surface (Fig. 10A) bears pronounced dorsal and ventral crests. The more dorsal of these is formed by the rounded course of the horizontal (lateral) semicircular canal. It ends anteriorly in a rounded prominence for the horizontal ampulla. In front of this is a similar prominence for the anterior ampulla, and that in turn continues into a rounded ridge marking the path of the anterior semicircular canal (Fig. 10A). A short triangular alar process extends anterodorsally. The ventral crest, passing from anteroventral to posterodorsal, is the well-developed crista prootica. The facial nerve (VII) foramen

exits below this, about halfway along its length (Fig. 10B).

The anteromedial surface of the prootic is divided into upper and lower parts by a rounded external ridge that marks the course of the utricle. Posteroventrally, this ridge is excavated by a small concavity (acoustic recess of Oelrich, 1956) from which open two foramina (Fig. 10B). The smaller anterior acoustic foramen carries vestibular branches of the vestibulocochlear nerve (VIII) from the ampullae of the semicircular canals and parts of the macular apparatus. The larger posterior foramen (posterior acoustic foramen of Oelrich, 1956) opens from the main chamber (cavum capsularis) and carries both vestibular (macular) and cochlear fibres of the vestibulocochlear nerve (VIII).

The posteromedial surface of the prootic is widest dorsally and tapers ventrally (Fig. 10C). It is bordered by articular surfaces for other parts of the otic capsule – the supraoccipital along the dorsolateral and anterodorsal margins, and the otooccipital posterolaterally (interrupted by the fenestra ovalis) and anteroventrally. The apex of the supraoccipital facet is perforated by the anterior semicircular canal, and the posterolateral otooccipital facet contains the horizontal (lateral) canal. Ventrally, the facets for the otooccipital converge at the point where the prootic meets the basal plate (sphenoid + basioccipital). The cranial surface may be divided roughly into dorsal (vestibular) and ventral (cochlear, lagenar) cavities. The dorsal cavum capsularis is smooth-walled but pierced anteriorly by the ampullary recess (ampullae of the ante-
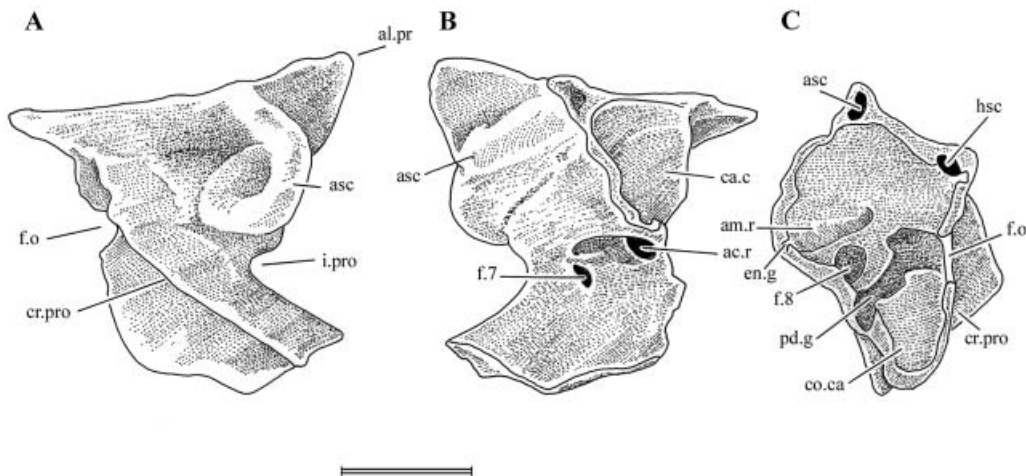
Figure 10. *Neusticurus ecpleopus*. Right prootic (MVZ 163394) in A, lateral; B, medial; and C, posteromedial views. Abbreviations: ac.r, acoustic recess; al.pr, alar process; am.r, ampullary recess (anterior and horizontal semicircular canals); asc, path of anterior semicircular canal; ca.c, cavum capsularis; co.ca, cochlear cavity; cr.pro, crista prootica; en.g, groove leading into canal for endolymphatic duct (enters supraoccipital); f.o, fenestra ovalis; f.7, facial foramen (cranial nerve VII); f.8, foramen for vestibulocochlear nerve (cranial nerve VIII); hsc, path for horizontal semicircular canal; pd.g, groove for perilymphatic duct. Scale bar = 1 mm.

rior and horizontal canals), from which a broad groove, carrying the utricle, extends posteriorly. In *Ctenosaura* (Oelrich, 1956), the dorsal cavum is separated from the ventral cochlear cavity (lagenar recess) by a crest, the cochlear or lagenar crest. In *Neusticurus ecpleopus*, however (and in *Cnemidophorus* and many other scleroglossans), the dorsal and ventral cavities are separated by a distinct groove (of variable depth), bounded dorsally by the cochlear crest. The groove runs ventral to the posterior acoustic foramen (the utricular groove runs dorsal to it), and then posteriorly onto the otooccipital. It carries the perilymphatic duct of the membranous labyrinth to the perilymphatic foramen. Unusually, the prootic in *N. ecpleopus* forms part of the border of this foramen, and also provides anterodorsal closure for the medial aperture of the recessus scalae tympani. Further dorsally, a small groove leads out of the utricular recess and into the supraoccipital facet. This runs into the small canal for the endolymphatic duct described above. As in most scleroglossans (Evans, in press), the fenestra ovalis is positioned well above the level of the basal plate, with a long opisthotic/prootic suture below it.

OTOOCCIPITAL (FIG. 11A–C)

The compound otooccipital is formed by the triangular exoccipital bone posteriorly and the opisthotic anteriorly. The exoccipital is a sturdy element, contributing a major portion to the occipital condyle and thus to the posterior surface of the braincase. The main body is pierced by two small hypoglossal nerve foramina. A small vagus foramen lies dorsally, between the exoccipital and opisthotic. It is closed ventrally by a con-

tact between the exoccipital and the posterior ampullary swelling. Below this is the large ovoid lateral opening of the recessus scalae tympani, closed ventrally by the basioccipital, although this element makes only a small contribution to the rim. The deepest and most expanded portion of the recessus scalae tympani lies dorsally, within the opisthotic. This is in marked contrast to the condition in most iguanians, where the deepest part of the recessus is ventral, within the basioccipital (Evans, in press).

Like the prootic, the opisthotic portion of the otooccipital is wide dorsally and tapers ventrally. Posterolaterally, the bone is extended into a short paroccipital process with a wide distal tip. This tip is capped by cartilage in the hatchling, gradually ossifying during post-hatchling ontogeny. The shortness of the process suggests limited metakinetic potential. At the base of the paroccipital process, there is a small but conspicuous pit (best seen from a posteroventral view; Fig. 11B) that appears to be associated with the attachment of a free epibranchial element of the hyoid apparatus (see below). The posterior surface of the bone carries a conspicuous rounded crest marking the course of the posterior semicircular canal. Seen in anterior view, the opisthotic mirrors the prootic, divided into a dorsal vestibular region, the cavum, and a ventral cochlear cavity (lagenar recess) that tapers to a point ventrally. The prootic and supraoccipital facets are perforated by the canals for the horizontal and posterior semicircular ducts, respectively. The cavum capsularis bears two medial openings, one above the other. The larger, inferior opening is the recess for the ampulla of the posterior semicircular canal. This large cavity is separated from the vestibular recess by a con-
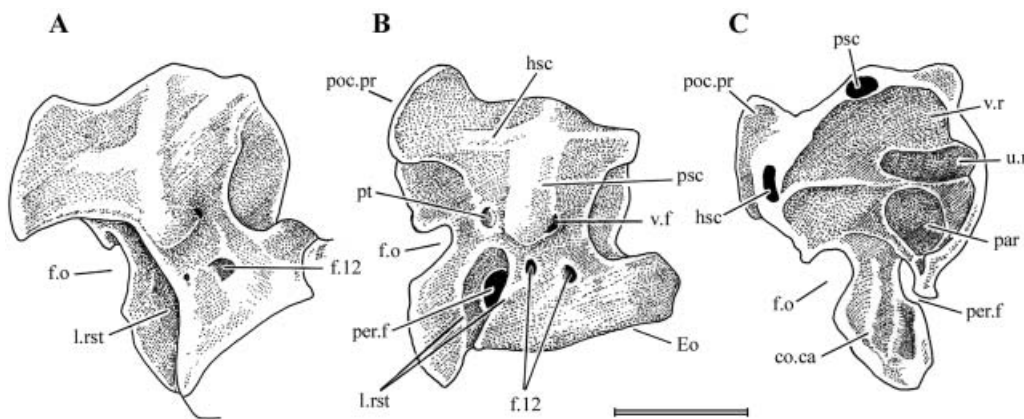
Figure 11. *Neusticurus ecpleopus*. Left otooccipital (MVZ 163394) in A, posterolateral; B, lateral; and C, anteromedial views. Note that the view in B is designed to show the perilymphatic foramen opening into the rst; the medial opening of the rst is out of the plane of view. Abbreviations: co.ca, cochlear cavity; Eo, exoccipital; f.o, fenestra ovalis; f.12, hypoglossal nerve foramina (cranial nerve XII); hsc, path of horizontal semicircular canal; l.rst, lateral aperture of recessus scala tympani; par, posterior ampullary recess; per.f, perilymphatic foramen; poc.pr, paroccipital process; psc, path of posterior semicircular canal; pt, pit for hyoid (see text); u.r, utricular recess, groove for horizontal semicircular canal leading toward utricle; v.f, vagus foramen (cranial nerve X); v.r, vestibular recess. Scale bar = 1 mm.

spicuous crest. Opening into the vestibular recess is a groove carrying the horizontal semicircular canal towards the utricular recess.

The triangular ventral (cochlear or lagenar) recess of the opisthotic is very delicate and forms a concave flange (Fig. 11C) below the cavum and separated from it by a continuation of the cochlear crest. This region is unusual in lacking a fully enclosed perilymphatic foramen. Instead, the anterior margin contains a notch that is closed by the prootic. The open medial margin of the perilymphatic foramen is continuous with the deep groove for the perilymphatic duct on the prootic, and the prootic contributes to the margins of both the perilymphatic foramen and the medial opening of the recessus scalae tympani.

STAPES

The stapes of *Neusticurus ecpleopus* has a relatively large footplate and a very slender shaft. A distinct cartilaginous internal (or quadrate) process is present throughout the ontogenetic series of cleared and stained specimens we examined. Wever (1978) reported the presence of an internal process in *Ameiva*, *Cnemidophorus* and *Tupinambis*, but he did not examine any gymnophthalmids. Estes *et al.* (1988) listed loss of the internal process as a possible synapomorphy of Gymnophthalmidae but material available to them included only a limited sample of *Echinosaura*, *Prionodactylus* and *Proctoporus*. Our

observations of *Neusticurus ecpleopus* indicate that the internal process is not uniformly lost within Gymnophthalmidae, and that a more detailed analysis of its distribution is needed.

THE LOWER JAW (FIG. 12)

DENTARY

The dentary is strongly built. It carries 19–21 tooth positions above a closed Meckelian fossa in which the upper and lower margins have fully fused to form a tube that extends back to the level of the penultimate tooth position (Fig. 12A). The alveolar margin of the bone is straight, whereas the ventral margin is gently curved. The symphysial surface is very small and limited to the upper half of the anterior jaw surface. The lateral surface of the dentary (Fig. 12B) carries a series of four nutrient foramina. Further posteriorly, the bone is overlapped by a large labial coronoid flange, below which it is extended into a posteroventral process that reaches the posterior level of the coronoid.

CORONOID

The coronoid is triradiate in medial view (Fig. 12A), with a narrow tapering dorsal process and strongly bifurcated anteromedial and posteromedial processes. The dorsal (coronoid) and posteromedial processes are
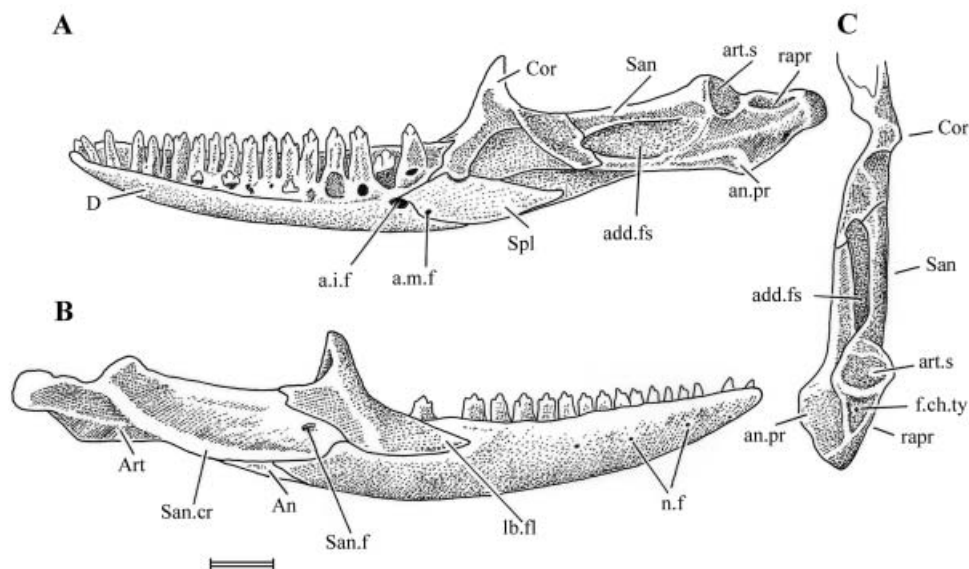
Figure 12. *Neusticurus ecpleopus*. Right lower jaw ramus (MVZ 163394) in A, medial; B, lateral; and C, partial dorsal views. Abbreviations: add.fs, adductor fossa; a.i.f, anterior inferior foramen; a.m.f, anterior mylohyoid foramen; An, angular; An.pr, angular process; Art, articular; Art.s, articular surface for quadrate; Cor, coronoid; D, dentary; f.ch.ty, foramen for chorda tympani branch of facial nerve (cranial nerve VII); lb.fl, labial flange of coronoid; n.f, nutrient foramina; rapr, retroarticular process; San, surangular; San.cr, surangular crest; San.f, surangular foramen; Spl, splenial. Scale bar = 1 mm.

linked by a medial crest that runs down the posterior border of the coronoid process and then along the anterior margin of the posteromedial process. The crest delimits an excavated area behind it for adductor muscle attachment. The posteromedial process also enters the anterior margin of the adductor fossa, but there is little development of a discrete surangular process (Fig. 12C). Laterally (Fig. 12B), the coronoid bears a very large, tongue-like labial process that extends forward to the level of the third tooth position from the rear. Together, the labial and anteromedial processes clasp the posterior end of the dentary.

SURANGULAR

The surangular is a robust bone that forms most of the lateral surface of the mandible behind the coronoid. Anterolaterally, it fits into a recess between the coronoid dorsally and the dentary ventrally, at which point its lateral surface is perforated by a large surangular foramen. Posteriorly, the surangular fuses with the articular/prearticular complex. The bone is limited ventrally by a strong, curving crest that divides it from the region of the prearticular and marks the line of attachment of the superficial adductor muscle. The crest is much weaker in juveniles.

ANGULAR

The angular is a very slender bone, confined to the ventral margin of the mandible. It extends from ventral to posterolateral, the latter part forming a small wedge between the dentary and the crested inferior margin of the jaw (Fig. 12B).

SPLENIAL

A small blade-like splenial lies on the medial surface of the mandible, between the closed end of the Meckelian fossa and the coronoid. Posteriorly, it reaches beyond the midpoint of the coronoid. Anteriorly, the bone is notched by a large anterior inferior foramen that is closed by the posterior margin of the Meckelian fossa. A smaller anterior mylohyoid foramen opens further posteroventrally.

ARTICULAR

The articular/prearticular complex forms the posteromedial and terminal parts of the jaw ramus. The prearticular component of the bone is angled so that its dorsal border lies more medially than its ventral one. This is due to the enlargement of the adductor fossa lying between the prearticular and surangular – a feature found also in teiids and lacertids (Estes *et al*., 1988; S. E. Evans, pers. observ.). Further poste-

riorly, the prearticular is almost horizontal in its orientation. The angulation becomes even more pronounced posteriorly, until the bone forms a ventromedially directed blade. This horizontal surface then continues posteromedially into a pronounced triangular angular process, the size of which increases with age/size. The articular surface for the quadrate is short and rounded, but the anterior surface is almost vertical, limiting forward movement of the quadrate.

The retroarticular process is relatively slender, with the tip inflected medially. It is perforated by a small foramen for the chorda tympani branch of the facial nerve. The process is cartilaginous in the hatchling. It first develops an apophyseal ossification on its posterolateral corner at 45.2 mm SVL, then one on its posteromedial corner at 47.6 mm SVL. These apophyseal ossifications begin to fuse at 51.1 mm SVL, and by 55.6 mm SVL the retroarticular process is completely coossified with the articular.

DENTITION

The tooth implantation is deeply pleurodont, with lingual replacement. The premaxilla bears small unicuspid teeth, but the teeth of the dentary and maxilla are strongly heterodont. The numbers of uni-, bi- and tricuspid teeth show some variation, as does the shape of the tricuspid teeth (deeper delimitation of the cusps in juveniles).

In the smallest specimen examined (22.4 mm SVL), the first few teeth of the maxilla and dentary are unicuspids, with one bicuspid among them. In the posterior parts of the tooth rows of the same specimen, the teeth are a mixture of unicuspids and tricuspids, suggesting that the unicuspids of the embryo are quickly replaced by bicuspids anteriorly and tricuspids posteriorly. There does, however, appear to be a difference between the maxillary and dentary dentitions.

In the maxilla, the variation in the numbers of tricuspid teeth is fairly limited (six to nine). The main variation is between the uni- and bicuspid teeth. Unicuspid numbers range from one to seven, although apart from MVZ 163389 (our smallest dry skull), most show between one and three. For the bicuspids, the range is from one to nine, but generally rises with increasing SVL. Essentially, this agrees with the suggestion made above, that in the embryo most teeth in the maxilla are unicuspid. These are replaced by bicuspids anteriorly and by tricuspids at the rear, with further tricuspid positions being added as the tooth row elongates posteriorly (from 14 teeth at hatching to 18 in the adult).

In the dentary, the pattern is slightly different. Although the number of tricuspids remains high throughout the sample (nine to 12), bicuspid numbers only increase slightly with age/size (typically three to

six), whereas the unicuspid numbers remain high (seven to nine). In maxillae of the same size, the unicuspids fall to only one to three in larger specimens, with the bicuspids rising to nine in number. The difference between the numbers of unicuspid teeth on the dentary and maxilla is partly accounted for by the five unicuspid teeth on the premaxilla (giving a combined upper jaw number approaching that of the dentary). However, the difference in the bicuspid number remains – five being the highest bicuspid count in the dentary, nine the highest in the maxilla.
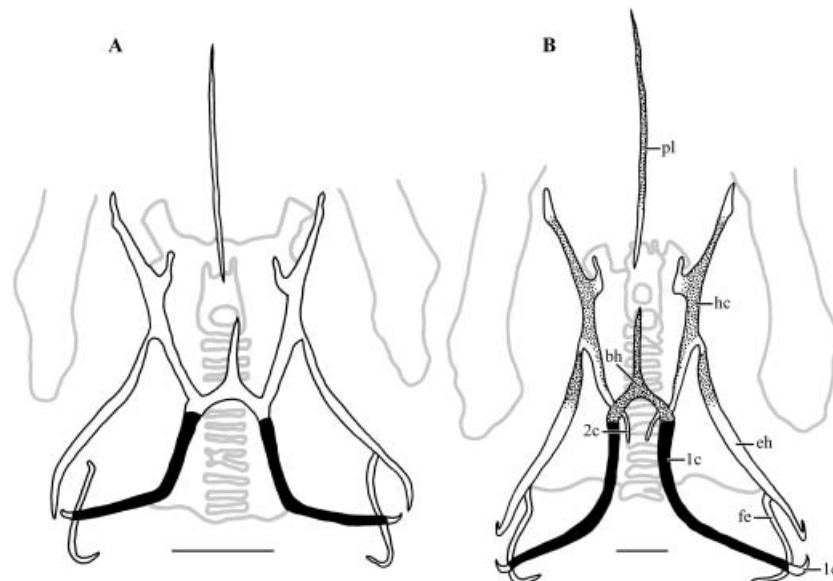
HYOID APPARATUS

The description of the hyoid apparatus is based on the cleared and stained specimens. The hyoid apparatus in adult *Neusticurus ecpleopus* is shown in Figure 13B. It consists of a central triradiate element, the basihyal, which extends anteriorly just past the posterior margin of the larynx, becoming progressively more slender before terminating in a point. It is heavily calcified in all but this anteriormost tip. The processus lingualis lies distal to the basihyal, separated from it (as in teiids, contra Presch, 1980) by a distance roughly one-quarter of the length of the basihyal. It is also heavily calcified, except in its rounded proximal and pointed distal ends. The processus lingualis extends anteriorly almost to the level of the midpoint of the dentary.

Three paired elements arise from the posterolateral processes of the basihyal. The hyoid cornu is an anteriorly and somewhat laterally directed element, with a medially directed, hook-shaped process at its midpoint. The cornu terminates distally at the level of the midpoint of the angular, in a slightly expanded foot with a laterally flattened edge. It is heavily calcified except at its distal end and medial process. In some individuals, a small, slender, uncalcified cartilage articulates with the posterolateral corner of the distal end of the hyoid cornu. The epihyal, moderately calcified proximally, extends posterolaterally from a well-defined articulation about one-third of the way up the lateral edge of the hyoid cornu. It becomes more slender distally, hooking sharply anterodorsally when level with the retroarticular process, terminating in a point shortly thereafter.

The next element to arise from the basihyal is the first ceratobranchial, the only element of the hyoid that is ossified. Proximally, it articulates with the basihyal via a rounded cartilaginous cap that may exhibit a calcification centre. The first ceratobranchial is a uniformly slender element that first projects directly posteriorly, then angles strongly laterally at the level of the atlas. It is capped distally by a first epibranchial that may be slightly calcified.

The last element to arise from the basihyal in *Neusticurus ecpleopus* is a rudimentary second ceratobranchial (contra Presch, 1980; see discussion below of

Figure 13. *Neusticurus ecpleopus*. Hyoid apparatus. Posterior end of mandible, anterior and posterior ends of braincase, larynx, and trachea are shaded to show relative position. Cartilage is white, calcified cartilage is stippled, and bone is black; A, hatchling, 22.4 mm SVL (KU 148246); B, subadult, 47.6 mm SVL (MVZ 174896). bh, basihyal; eh, epihyal; fe, free epibranchial; hc, hyoid cornu; pl, processus lingualis; 1c, first ceratobranchial; 1e, first epibranchial; 2c, second ceratobranchial. Scale bars = 1 mm.

ontogenetic changes in the hyoid apparatus). Positioned medial to the first ceratobranchial, it is a slender element that measures roughly one-third the length of the basihyal, lacks an associated epibranchial and is moderately calcified in all but its distal tip.

The final element of the hyoid apparatus is an uncalcified cartilage (free epibranchial of Cope, 1900; Savage, 1963) embedded in the side of the neck, with no connection to the rest of the hyoid. It is a slender, sigmoid structure that lies, in ventral view, beneath the epihyal and first epibranchial. Posteriorly, it hooks dorsomedially, terminating in a free pointed tip. Proximally, it curves gently dorsally to insert into a small pit in the otooccipital, near the base of the paroccipital process (Fig. 11B, pt). MacLean (1974: 191–192) noted the presence of a 'disjunct epi-element' in 'many' gymnophthalmids, but described it as attaching posteriorly to the epihyal. Tanner & Avery (1982) considered this element to be unique to xantusiids, but our survey indicates that it is more widespread that this (see below).

The morphology of the hatchling hyoid apparatus is shown in Figure 13A. The second ceratobranchial is absent in six of the 22 cleared and stained specimens examined. All six fall within the first 20% of the postnatal size range, suggesting that their absence may be an ontogenetic phenomenon. In addition, owing to their variable degree of development, narrow point of articulation with the basihyal and poor calcification, the second ceratobranchials probably rarely survive the skeletonization process. Presch (1980) stated that second ceratobranchials are absent in *Neusticurus*, but he examined only three *N. ecpleopus*.

All other elements of the hyoid apparatus are present throughout the postnatal ontogeny of *Neusticurus ecpleopus*, and considerable allometric change is evident between the hatchling and adult morphologies. Overall, the hyoid apparatus narrows and elongates ontogenetically. Although the basihyal maintains a position roughly level with the posterior end of the lower jaw, the anterior process of the basihyal lengthens, displacing the processus lingualis anteriorly. In this displacement, the gap between the anterior process of the basihyal and the processus lingualis maintains its position ventral to the larynx. The processus lingualis retains a roughly 3/1 proportion to the length of the basihyal including its anterior process. The posterolateral processes of the basihyal are more posteriorly directed in the adult than in the hatchling, paralleling the observation made by MacLean (1974) that these processes in teiids are more posteriorly directed than in gymnophthalmids.

The anterior extension of the hyoid cornu well beyond the origin of the epihyal, noted by MacLean (1974) as a distinguishing feature of teiioids, is already well developed in hatchling *Neusticurus ecpleopus*. The medial process is also present, but becomes more robustly developed in the adult. Little change appears to characterize the epihyal, except that it is less laterally divergent in the adult than in the hatchling.

One of the most striking ontogenetic changes in the hyoid apparatus involves the lateral angulation of the first ceratobranchial, which is much more acute in the hatchling than in the adult. MacLean (1974) noted the strong angulation of the first ceratobranchials in gymnophthalmids, and Estes *et al*. (1988) considered it to be a synapomorphy of this group. Hoyos (1998) subdivided this character into two states, lateral angulation greater than 90°, and lateral angulation equaling 90°. Because angulation of the first ceratobranchial decreases in ontogeny, at least in *Neusticurus ecpleopus*, care must be taken to score such a character only in comparably mature semaphoronts.

In the hatchling, the shaft of the first ceratobranchial is already fully ossified, and endochondral calcification is present throughout the basihyal, in the hyoid cornu, and in the proximal portion of the epihyal. Calcification first appears in the processus lingualis at 33% maximum size (23.6 mm SVL). It appears in the cartilage capping the proximal end of the first ceratobranchial and in the first epibranchial at 66% maximum size (47.6 mm SVL), but occurs only irregularly in the latter. Calcification does not appear in the second ceratobranchial until 82% maximum size (59.1 mm SVL), and is never observed in the free epibranchial.

The hyoid apparatus of *Neusticurus ecpleopus* differs both in morphology and mineralization from that in *N. rudis* (as discussed and illustrated by Beebe, 1945). In the former the processus lingualis is detached from the basihyal whereas in the latter it is continuous with it. The hook-shaped process on the medial edge of the hyoid cornu is more robust and more proximally located in *N. ecpleopus* than in *N. rudis*. The epihyal is more posteriorly directed and less calcified in *N. ecpleopus* than in *N. rudis*. The second ceratobranchial, when present, is much less robust in *N. ecpleopus* and lacks the calcification seen in *N. rudis*. Perhaps the most striking difference is the abrupt lateral angulation of the first ceratobranchial in *N. ecpleopus* in contrast to its gradual angulation in *N. rudis*. Beebe (1945) did not report the presence of a free epibranchial in *N. rudis*.

INTRASPECIFIC VARIATION

Relatively little work has been published on intraspecific variation in the lizard skull, despite the importance of cranial characters in classification. The principal recent studies have been those of Rieppel &

Crumly (1997) on the chameleon skull, and Barahona & Barbadillo (1997, 1998) on lacertids. These authors found that the characters that varied to the greatest degree between related genera and species were also those that varied during ontogeny. Examination of intraspecific differences in *Neusticurus*, albeit in a limited sample, suggests the same is true for this group. Intraspecific variation includes ontogenetic, individual and sexual differences. We have no data on the latter, but in the sections above, we provided discussion of various aspects of the former two. Results of those observations are summarized here.

The main differences between juvenile and adult *Neusticurus ecpleopus* relate to the firmness of the articulation (greater overlap) between the bones of the dermatocranium (nasal/premaxilla, nasal/frontal, frontal/parietal, etc.; Fig. 6), greater thickness of individual bones, and generally more elongated or expanded processes (longer anterior processes of the squamosal and supratemporal; longer and more distally expanded basipterygoid processes of the basisphenoid; longer posterior processes of the postorbital and parietal). In addition, the frontal of the adult is relatively wider posteriorly, whereas the parietal table and postparietal processes elongate, and the parietal table narrows (Figs 1, 6). The quadrate process of the stapes, initially terminating as a single process, becomes distinctly forked in the adult. The hyoid apparatus narrows and elongates through ontogeny; lateral angulation of the first ceratobranchial is more acute in hatchlings than in adults, and the second ceratobranchial is absent in early postnatal stages.

OVERVIEW OF THE SKULL OF *NEUSTICURUS* IN COMPARISON WITH THAT OF OTHER TEIIOIDS

The skull of *Neusticurus ecpleopus* can be regarded as generally representative of the Gymnophthalmidae (fused frontals, frontal lappets over parietal, loss of parietal foramen, quadrate process on stapes; Estes *et al*., 1988). There are, however, a number of key areas where variation in skull configuration of gymnophthalmids is pronounced. These include preorbital length; the morphology of the upper temporal and suborbital fenestrae; the morphology of the frontal, parietal, squamosal and palatal elements; the presence or absence of discrete lacrimals, postorbitals and postfrontals; tooth counts; and the morphology of the braincase and lower jaw.

Typically, the gymnophthalmid preorbital region is rather elongated, and the upper temporal and suborbital fenestrae remain open. However, preorbital shortening occurs in some taxa (e.g. *Bachia*, *Colobodactylus*, *Leposoma*), whereas the upper temporal fenestrae range from fully open (e.g. *Anadia*, *Cerco-* *saura*, *Euspondylus*, *Proctoporus*), to reduced (*Colobosaura*, *Opipeuter*, *Pholidobolus)* or closed (*Alopoglossus*, *Bachia*, *Gymnophthalmus*, *Leposoma*). Closure of the upper temporal fenestrae is presumably functional, and is paralleled in other lizard groups (e.g. lacertids, scincids), but it still lacks a compelling explanation. In the palate, the suborbital fenestrae may also be reduced by expansion of the palatine (*Bachia*) or ectopterygoid (some *Euspondylus*). Similarly, the length of the interpterygoid vacuity is variable. In *Echinosaura* and *Opipeuter* it reaches forward to the level of the vomers, but it often ends between the palatines, as in *Neusticurus*.

Individual bones, of course, show a greater degree of variation. Gymnophthalmid nasals are usually at least partially separated by the broad dorsal process of the premaxilla (as in *N. ecpleopus*), but this separation may be complete where the premaxilla meets the frontal (many *Alopoglossus*, some *Bachia*, *Echinosaura*). Similarly, whereas *N. ecpleopus* shows a typical gymnophthalmid frontal pattern with a strongly trifurcate anterior margin (also seen in *Leposoma*, *Proctoporus*), this margin may appear tapered (e.g. some *Bachia*, some *Gymnophthalmus*) or U-shaped (*Alopoglossus*, some *Gymnophthalmus*) with loss of either the anterolateral or the median processes, respectively. Ventrally, the cristae cranii show two distinct patterns. In most genera, including *Neusticurus*, the frontal is narrow and the cristae meet ventrally to create a strong, tubular structure; Estes *et al*. (1988) listed this amongst the synapomorphies of gymnophthalmids. In some genera, however (e.g. *Arthrosaura*, *Bachia*, *Colobodactylus*, *Gymnophthalmus*, *Leposoma*), the frontal is broader and the cristae are only weakly developed. This condition resembles that of teiids, but whether it is primitive or derived for gymnophthalmids is difficult to judge. Where the cristae are weak, an elongated posterior process of the prefrontal strengthens the orbital margin by approaching or meeting the postfrontal. The gymnophthalmid parietal is fairly uniform in shape, but the skull table and the postparietal processes vary in length according to adult size (mirroring the ontogenetic changes described for *N. ecpleopus*). There is never a parietal foramen and only rarely (e.g. *Colobosaura*, *Leposoma*) does a lateral parietal shelf contribute to the closure of the upper temporal fenestra.

As in *Neusticurus*, the single premaxilla typically has a broad, flared nasal process with strong posterior facets for the nasals; more rarely the dorsal process is narrow (e.g. *Gymnophthalmus speciosus*). The maxilla bears a wide medial shelf that overlaps the vomer to separate the vomeronasal opening from the choana. In the choanal rim, the shelf may contain a distinct notch, as in *Neusticurus ecpleopus* (MCV 163427), but the function of this feature is not known. Moreover, in

Alopoglossus buckleyi (MCZ 163438), the notch is converted into a discrete foramen by the anterior expansion and apposition of the palatine. Maxillary tooth counts range from 10 to 55 (MacLean, 1974; Presch, 1980), with the lowest counts in *Bachia* and the highest in *Alopoglossus* and *Ptychoglossus*, although as in *Neusticurus*, most counts lie in the range of 20–30. Gymnophthalmid teeth are often unicuspid or bicuspid (recurved in *Bachia*), but in several genera (e.g. *Cercosaura*, *Neusticurus*, *Proctoporus*) the posterior teeth approach tricuspidy by developing accessory cusps.

There is no free lacrimal in the adult of *Neusticurus ecpleopus* and this is true of many other genera (e.g. *Cercosaura*, *Gymnophthalmus*, *Proctoporus*). Where present (e.g. *Alopoglossus*, *Bachia*, *Colobosaura*), the bone can be very small and could easily be overlooked (e.g. *Echinosaura*, *Euspondylus*). The postfrontal and postorbital are closely integrated and clearly form a functional unit. Fusion sometimes occurs (e.g. *Alopoglossus*, *Heterodactylus*; Presch, 1980). Where discrete, the postfrontal is typically tri- or quadriradiate (*Neusticurus*), but in *Anadia*, *Bachia*, *Gymnophthalmus* and *Leposoma*, it expands posteriorly into the narrow upper temporal fenestra. In *Alopoglossus* and *Heterodactylus* (Presch, 1980), the single postorbitofrontal closes the fenestra. The squamosal of *Echinosaura* (Kizirian, 1996) bears a small dorsal process like that of teiids, but most gymnophthalmids have the typical 'hockey-stick' shape found in other squamates. The gymnophthalmid quadrate is usually large, with a broad conch and a distinct tympanic crest (as in *Neusticurus ecpleopus*), but in some burrowers (e.g. *Anotosaura*, *Bachia*; MacLean, 1974) the tympanic membrane is lost and the quadrate is correspondingly reduced.

Gymnophthalmid vomers are narrow, and may be paired, partly fused (as in *Neusticurus*) or fully fused (e.g. *Anadia*), although this feature is probably subject to variation within and between species. In some taxa (e.g. *Alopoglossus*, *Bachia*), the maxillary process of the palatine has an anteromedial contact with the vomer, excluding the maxilla from the choanal margin. Gymnophthalmid pterygoids are typically gracile, like those in *N. ecpleopus*, but vary in being either strongly (e.g. *Anadia*, *Gymnophthalmus*) or weakly (e.g. *Proctoporus*) bifurcated anteriorly depending on the size of the suborbital fenestra. Pterygoid teeth are retained in some species of *Arthrosaura*, *Colobosaura*, *Gymnophthalmus* and *Ptychoglossus* (Presch, 1980) but generally are lost.

Neusticurus ecpleopus is the only gymnophthalmid to be described on the basis of both articulated and disarticulated material. This particularly limits comparisons of the braincase, because braincase sutures are often obscured and the internal anatomy is poorly

known. The parasphenoid rostrum is narrow and fully ossified in *Neusticurus* (and *Proctoporus*) but remains unossified in some genera (e.g. *Gymnophthalmus*, *Leposoma*). Similarly, the basipterygoid processes range from short and distally expanded like those of teiids (*Anadia*, *Gymnophthalmus*) to long and narrow (*Leposoma*, *Proctoporus*), although the shape varies considerably with age. In *Bachia*, for example, the tips are very small and metakinetic movement is unlikely. *Proctoporus ventrimaculatus*, at least, resembles *Neusticurus ecpleopus* in that the endolymphatic duct exits from the prootic. In many genera (e.g. *Leposoma*), the otooccipital has a reduced paroccipital process. The stapes shows a tendency towards reduction of the shaft and enlargement of the footplate in the smaller genera (e.g. *Bachia*, MacLean, 1974; *Proctoporus*), and Presch (1980) reported finding an extrastapedial bone in *Bachia* and *Heterodactylus*. Estes *et al.* (1988) listed the loss of the quadrate (internal) process of the stapes as a derived feature of gymnophthalmids, but this was based on examination of only three genera, *Echinosaura*, *Prionodactylus* and *Proctoporus*. We found the process in *Neusticurus ecpleopus*, despite the possibility that *Echinosaura* and *Neusticurus* may be congeneric (Kizirian, 1996).

The lower jaw of *Neusticurus ecpleopus* is representative of the gymnophthalmid mandible generally. Dentary shape varies from long and shallow (*Gymnophthalmus*) to short and deep (*Bachia*), although a ventrolateral extension of the dentary usually braces the posterior part of the mandible. As in *Neusticurus*, the Meckelian fossa is commonly closed by fusion of its own dorsal and ventral edges (e.g. *Anadia*, *Echinosaura*, *Euspondylus*, *Proctoporus*), but the fossa sometimes remains open (e.g. *Alopoglossus*, *Bachia*, *Colobodactylus*, *Colobosaura*, *Gymnophthalmus*). The splenial is retained as a discrete element, but whereas in some taxa it is an elongate bone (e.g. *Bachia*, *Colobodactylus*, *Ptychoglossus stenolepis*), in many it is reduced to a small posterior plate beneath the rear of the tooth row (e.g. *Anadia*, *Neusticurus*, *Proctoporus*). Rarely (e.g. *Ecpleopus affinus*, *Neusticurus strangulatus*), the splenial may fuse with the angular. Where separate (e.g. *Anadia*), the angular is reduced to a short, narrow ventrolateral splint.

The more generalized gymnophthalmids, like *Neusticurus ecpleopus*, resemble small extant teiids in many cranial characters, including the general elongation of the preorbital region, open temporal fenestrae and complete skull arches, incompletely neochoanate palate, fusion of the frontals, loss of the parietal foramen (and general parietal shape), gracile pterygoid and, in the lower jaw, the presence of a prominent prearticular crest with an embedded angular process, and a deep surangular fossa (Estes *et al.*, 1988). This latter feature is shared by teiids, lacertids

and gymnophthalmids, and results from the possession of an anterior extension of the posterior adductor muscle into the Meckelian fossa deep to the splenial. There are other detailed similarities between these three families (the Lacertiformes of Estes *et al*., 1988). On the medial surface of the maxilla, a sharp ridge separates the anterodorsal region from the recessed posteroventral part of the bone. The ridge gives attachment to connective tissue separating the nasal sac from the more ventrally placed nasolacrimal duct (C. J. Bell & S. E. Evans, pers. observ., *Cnemidophorus*). Lacertiforms also share the presence of a distinct pit on the otooccipital for the tip of the free second epibranchial, although this feature is more obvious in small teiids than in large teiids. As far as we are aware, this is the first report of a novel character, and a more detailed survey of its distribution is currently underway (S. E. Evans, J. A. Maisano & C. J. Bell, unpubl. data). There is also a common palatal structure in which the medial borders of the palatines extend ventrally to convert the vacuity into a deep pyriform recess and to separate the deep choanal grooves that converge towards the midline.

Teiids differ from gymnophthalmids in retaining a comparatively large lacrimal that lies between the prefrontal and jugal in the anterior orbital margin, whereas the postorbital and postfrontal are fused in most adult teiids (separate in *Callopistes*, *Tupinambis* and some *Teius*). In many teiids (*Ameiva*, *Kentropyx*, *Teius*; variably in *Callopistes*, *Cnemidophorus* and *Dracaena*), but few gymnophthalmids, the squamosal resembles that of iguanians in the presence of a conspicuous dorsal process. In the teiid mandible, the Meckelian fossa always remains open (in contrast to many gymnophthalmids), and the splenial is always large, as is the angular.

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Doan TM. 2003. A new phylogenetic classification for the gymnophthalmid genera *Cercosaura*, *Pantodactylus* and *Prionodactylus* (Reptilia: Squamata). *Zoological Journal of the Linnean Society* **137:** 101–115.

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APPENDIX 1

NEUSTICURUS ECPLEOPUS SPECIMENS EXAMINED

Dry skulls. Collected in Peru (mostly in the Rio Cenepa area, except as indicated); measurements are from tip of premaxilla to posterior edge of supraoccipital: MVZ 163395, 11.7 mm; MVZ 163397, 12 mm; MVZ 163389, 12.1 mm; MVZ 174957, 12.2 mm (Rio Santiago); MVZ 163390, 12.3 mm; MVZ 174956, 13.5 mm (Rio Santiago); MVZ 163400, 14 mm; MVZ 163388, 14.5 mm; MVZ 163395, 15.1 mm; MVZ 163410, 16.1 mm; and MVZ 163394, disarticulated.

Cleared and double-stained specimens. Specimen SVLs are followed by sex, where known, and percentage maximum size based on that reported for each sex by Sherbrooke (1975) (average of male and female maximum sizes used to calculate percentage in specimens where sex is unknown): KU 48246, 22.4 mm SVL (33%), Napo, Ecuador; USNM 316870, 22.9 mm SVL (34%), Amazonas, Peru; KU 109803, 23.6 mm SVL (35%), Napo, Ecuador; MVZ 163166, 23.6 mm SVL (35%), Peru; KU 148251, 25.8 mm SVL (male, 36%), Napo, Ecuador; MVZ 174949, 26.7 mm SVL (40%), Peru; KU 109781, 27.3 mm SVL (male, 38%), Napo, Ecuador; MVZ 174920, 28.7 mm SVL (female, 46%), Peru; KU 109809, 28.9 mm SVL (female, 47%), Napo, Ecuador; MVZ 174928, 30.5 mm SVL (female, 49%), Peru; MVZ 174905, 31.8 mm SVL (female, 51%), Peru; KU 109789, 32.9 mm SVL (female, 53%), Napo, Ecuador; MVZ 163147, 34.3 mm SVL (male, 48%), Peru; MVZ 174901, 37.9 mm SVL (57%), Peru; MVZ 174899, 39 mm SVL (female, 63%), Amazonas, Peru; MVZ 163185, 40.7 mm SVL (female, 66%), Peru; MVZ 174953, 45.2 mm SVL (male, 63%), Amazonas, Peru; MVZ 174896, 47.6 mm SVL (female, 77%), Peru; MVZ 163187, 51.1 mm SVL (male, 71%), Amazonas, Peru; MVZ 163145, 55.6 mm SVL (male, 77%), Amazonas, Peru; MVZ 163202, 59.1 mm SVL (female, 95%), Peru; MVZ 174891, 63.2 mm SVL (male, 88%), Amazonas, Peru.

APPENDIX 2

ADDITIONAL GYMNOPHTHALMID AND TEIID SPECIMENS EXAMINED

Gymnophthalmidae. *Alopoglossus atriventris*, MCZ 45781; *A. buckleyi*, USNM 163438; *A. festae*, USNM 163423; *Alopoglossus* sp., USNM 319228; *Anadia bitaeniata* MCZ 146399; *Bachia heteropa*, USNM 248783; *B. intermedia*, MCZ 85537; *B. peruana*, CAS 93227; *Cercosaura ocellata*, MCZ 126876; *Colobodactylus tannayi*, MCZ 37394; *Colobosaura mentalis*, MCZ 59266; *Echinosaura horridis*, MCZ 18858; *E. panamansis*, CAS 99994; *Ecpleopus affinis*, USNM 163446; *E. gaudichaudi*, MCZ 59276; '*Euspondylus*' (= *Ptychoglossus*) *brevifrontalis*, MCZ 42134; *E. ?simonsii*, MCZ 45894; *Gymnophthalmus speciosus*, CAS 98968, *G. underwoodi*, MCZ 66943; *Leposoma parietale*, USNM 163430; *Neusticurus strangulatus*, USNM 163426, USNM 163427; *Opipeuter xestus*, CAS 80912; *Pholidobolus montium*, USNM 163441; *Proctoporus anatoloros*, USNM 163434, USNM 163435, *P. ?unicolor*, USNM 163428; *P. ventrimaculatus*, NAUQSP-JIM 0713, NAUQSP-JIM 0727, CJB 0571.

Teiidae. *Ameiva undulata*, CAS 68659; *Ameiva* sp., CJB 591; *Callopistes flavipunctatus*, MVZ 82409; *C. maculatus*, CJB 607; MVZ 175857; *Cnemidophorus deppei*, CAS 68970; *C. tigris*, CAS 174441, CJB 709; *Dracaena guianensis*, CAS 225062, CJB 0028; *Kentropyx pelviceps*, MVZ 163406, MVZ 163407; *Tupinambis teguixin*, CJB 601; *Tupinambis* sp., CJB 0021, CJB 0333.