

**A review of the leaf-nosed bats
Rhinonycteris, *Cloeotis* and *Triaenops*
(Chiroptera: Hipposideridae)**

by

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Introduction

The hipposiderid bats *Rhinonycteris* of northwestern Australia, *Cloeotis* of Africa and *Triaenops* of southwestern Asia and Africa form a small group characterised principally by a number of common features of the nasal foliations. All have a strap-like projection extending forward from the internarial region over the anterior leaf (of which it forms a part) to its edge and all have a strongly cellular posterior leaf, recalling in some of its features the cellular lancet of *Rhinolophus*. The posterior leaf in *Cloeotis* and *Triaenops* is further modified by three upwardly directed processes developed from its upper edge: in *Rhinonycteris* such processes are lacking, the upper part of the posterior leaf instead divided medianly, the division demarcated laterally by the thickened posterior walls of the uppermost cells.

The noseleaves of the three genera differ widely from those of the remaining hipposiderid genera *Hipposideros*, *Anthops*, *Asellia*, *Aselliscus*, *Coelops* and *Paracoelops*. None has an anterior median strap-like process or 'sella' although in *Hipposideros jonesi*, *H. marisae* and *H. ridleyi* the internarial septum is expanded to form a small circular structure between and above the nostrils, and none has a cellular posterior leaf, although it may be divided by vertical septa to form a shallowly pocketed structure, sometimes with a lobed upper margin. In no case, however, do these pockets form the deep, well divided cells that characterise *Rhinonycteris*, *Cloeotis* or *Triaenops*, nor do the lateral cells extend behind the upper part of the leaf as they do in the latter two of these genera. Vertical projections from the posterior leaf occur in *Asellia* and *Aselliscus* but are essentially lobulations of its upper margin rather than processes developed from the main body of the leaf as in *Cloeotis* and *Triaenops*. Moreover, the intermediate part of the noseleaf in *Rhinonycteris*, *Cloeotis* and *Triaenops* bears a well-developed anteriorly directed median process lacking from all other hipposiderids except the members of the *Hipposideros cyclops* group, but in these it is not

associated with a deep median cell in the posterior leaf as it is in *Rhinonycteris* and *Triaenops* and to a lesser extent in *Cloeotis*.

Historically, Gray (1866) first recognised the essential features of the noseleaf of *Rhinonycteris* in drawing attention to the then unique cellular structure of the posterior leaf and to the longitudinal strap-like process over the centre of the anterior leaf. These led him to divide it from the rhinolophids or Rhinolophina as the sole member of a separate group, the Rhinonycterina. Interestingly, his definition of this last group would also include the more recently described genera *Triaenops* and *Cloeotis*. Gray also recognised the features of the posterior leaf that characterise *Hipposideros*, and that separate this genus from *Asellia*, *Aselliscus*, *Coelops* and *Paracoelops*.

The genera *Rhinonycteris* and *Triaenops* were described and illustrated in some detail by Dobson (1878) while Peters (1906) provided further illustrations. Thomas (1901) and Hayman (1960) gave accounts of *Cloeotis* and indicated its several similarities with *Triaenops*. Tate (1941) briefly discussed the three genera and provided comparative notes on several of their structures, but was unable to make a direct examination of *Rhinonycteris*. No other detailed comparative account has appeared.

All measurements are in millimetres. Minimum and maximum values are given, preceded in parentheses by the total of specimens measured.

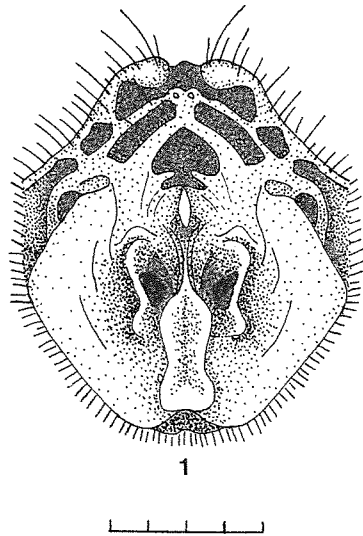


Fig. 1. *Rhinonycteris aurantius*. BM(NH) 57.10.24.10. Anterior view of noseleaf. Scale = 4 mm.

Systematic accounts

Genus *Rhinonycteris* Gray, 1847

Rhinonycteris Gray, 1847: 16. — *Rhinolophus aurantius* Gray, 1845. Mis-spelling.
Rhinonycteris Gray, 1866: 81. — *Rhinolophus aurantius* Gray, 1845.

Muzzle rather obtuse, flattened laterally; noseleaf large, completely covering muzzle, the anterior leaf more or less pentagonal in outline, overlying a single, much thickened fleshy supplementary leaflet or ridge that extends unbrokenly from the base of the posterior leaf beneath the anterior leaf but with a shallow emargination at the median line. Lateral margins of anterior leaf rather angular, the leaf widest at about the level of the nostrils, rounded anteriorly and deeply emarginate medianly, the leaf behind the emargination flexed upwards to form and support the anterior part of a horizontal, flattened longitudinal process that terminates posteriorly between the nostrils. This process arises posteriorly from the internarial septum and thus extends forward over the anterior part of the anterior leaf of which it forms a part, with its lateral margins sharply constricted at about one third of its length from the front to give it in plan an hour glass shape, the lateral margins slightly elevated to produce a gutter-like appearance from above. Intermediate part of leaf not much developed but with a prominent, long, narrow median process with rounded tip projecting forward and upwards from its centre, a deep, upward opening pit behind and above its base, partially divided from the large median cell of the posterior leaf.

Posterior leaf with deep central cell, the opening subconical in shape, its lower margin incomplete and divided medianly, conjoined to the deep pit behind median projection of intermediate leaf; central cell flanked on its outer sides and above by two lateral, narrow, longitudinal cells, each extending upwards to a fleshy median division that extends vertically as a slight projection; below each longitudinal cell two small cells, open basally. Beyond this band of cells and above each eye a row of three smaller cells on each side, the lowermost open basally, the uppermost pair incompletely delimited at the innermost margin, their posterior walls thickened at this point, margining the median longitudinal opening of a depression behind the posterior leaf. Lateral supplementary leaflet thickened and ridge-like, especially laterally, joining an extension from the rear wall of the prominent longitudinal cells of the posterior leaf, just anterior to the eye.

Ear triangular, sharply pointed, about same length as head or slightly less, tip acutely pointed, anterior margin slightly convex, posterior margin straight distally, then convex, a little thickened at antitragal lobe; lips fringed anteriorly by small warts or papillae; calcar about one third length of uropatagial margin.

Skull slender, slightly elongate; braincase wide posteriorly but narrower and elongate anteriorly; no obvious lambdoidal ridges; sagittal crest of unusual form, arising posteriorly at centre of hinder part of braincase, rising to a maximal height rather in advance of middle of braincase at a point about level with posterior zygomatic roots, then terminating abruptly in a forwardly curving projection that does not extend at all onto the moderately constricted postorbital region. Rostrum distinctly lower than braincase, with prominent inflations separated by a shallow trough that is deepened posteriorly to form a shallow depression delimited by very faint supraorbital ridges; anteorbital foramen very large, rounded, closed by a narrow, thin bar of bone; zygoma with greatly enlarged jugal projection occupying almost its entire length and extending upwards at least to the level of the upper insertion of the anteorbital bar, its anterior edge nearly straight, its apex rounded and its posterior margin slightly convex. Premaxillae unusually thick, with at their line of contact a distinct ridge on the upper face, terminating anteriorly in an upwardly and backwardly directed point; premaxillae making a V-shaped junction with the maxillae; anterior palatal foramina almost enclosed by delicate anterior premaxillary processes; palation wide, broadly U-shaped, no bony post-palate; sphenoidal bridge moderate, not concealing lateral apertures; shallow sphenoidal depression; cochleae not enlarged, their width about one and one half times their distance apart.

Dental formula $i\ 1/2$, $c\ 1/1$, $pm\ 2/2$, $m\ 3/3 = 30$. Upper incisor (i^2) bilobed, the outer lobe slightly the smaller; c^1 slender, with slight cingulum but with large posterior secondary cusp extending halfway along shaft; anterior upper premolar (pm^2) small, extruded, second upper premolar (pm^4) and c^1 in contact; m^3 little reduced, with metacone and trace of fourth commissure; i_{1-2} tricuspid, little imbricated; c_1 slender; anterior lower premolar (pm_2) about one half crown area and height of second lower premolar (pm_4); m_3 unreduced, its posterior triangle slightly larger than its anterior triangle.

Humerus with trochiter nearly as large as trochin, extending considerably beyond ovate humeral head, separated from it by a deep groove that terminates in a deep, well-developed supraglenoid fossa; articular surface on inner face of trochiter; strong median deltoid crest displaced towards rear of trochiter; capitellum slightly displaced from line of shaft, its principal articular surface large, rounded, lateral surface and trochlea narrow, about one quarter to one third width of principal surface; epitrochlea small, little more than one third width of articular surfaces, but with strong distal process from its distal margin, only narrowly separated from the trochlea and extending considerably beyond the articular surfaces.

The genus is monospecific and is of restricted distribution, occurring certainly only in northwestern Australia. The peculiarities of its noseleaf and skull remove it sharply from *Hipposideros* and its close relative *Anthops*, or

from the lines of variation presented by *Asellia* and *Aselliscus* or *Coelops* and *Paracoelops*.

***Rhinonycteris aurantius* (Gray, 1845)**

Rhinolophus aurantius Gray, 1845: 405, pl. 1, fig. 1. Port Essington, Northern Territory, Australia.

The species is sometimes brightly orange in overall colour, or sometimes brownish. Measurements: length of forearm (5) 45.8 – 47.1; greatest length of skull to canine (1) 17.1; condylocanine length (1) 14.8; width of rostrum (4) 5.5 – 5.8; postorbital width (2) 2.5, 2.6; zygomatic width (2) 8.5, 8.7; width of braincase (1) 7.5; mastoid width (1) 8.5; $c - m^3$ (5) 5.8 – 6.1; $c - m_3$ (5) 6.1 – 6.4.

There are certain records of this species from the Northern Territory (Parker, 1973: 35, 38, map 33; Johnson, 1964: 474) and from northern Kimberley in Western Australia (Ride, 1970: 166). It was reported from South Australia by Wood Jones (1925: 449) but its occurrence in this State is doubtful according to Ride (1970: 166, footnote, 148, footnote) who thinks that the report may originate from the period when the Northern Territory formed part of South Australia. Aitken (1975: 10, 13) noted that it is doubtfully recorded from South Australia, and suggested that it is uncertain whether it should continue to be included in the fauna of that State.

Genus *Cloeotis* Thomas, 1901

Cloeotis Thomas, 1901: 28. — *Cloeotis percivali* Thomas, 1901.

Muzzle broad, short and rather flat; noseleaf small, not covering muzzle, with two lateral supplementary leaflets. Anterior leaf narrow, not concealing lateral leaflets, its lateral margins indented at the level of the nostrils, its anterior margin rounded, with deep, narrow median anterior emargination; as in *Rhinonycteris* anterior part of leaf behind this emargination flexed upward to support and form part of a narrow, tongue-shaped longitudinal median horizontal process extending from the internarial septum over the anterior leaf. In plan view this process is narrow posteriorly, wide centrally and is forked anteriorly to form two small, narrow, parallel, sharply pointed projections lying over the median emargination of the anterior leaf, connected posteriorly by their supporting integument to the edges of the emargination. Nostrils deeply pocketed, with well-defined lateral lappets; intermediate leaf swollen laterally, with medianly a small but perfectly distinct projection that has a sharply pointed, vertically directed tip. Posterior leaf complex, tridentate, with basally a semicircle of six shallow cells surrounding the upper margin of the intermediate leaf, separated from each other by moderately fleshy septa, the outermost cells not enclosed basally, the

central pair the largest, the three projections from the upper part of the leaf lying above them. Of these the central projection is the largest, lying above and an extension of the dividing septum between the central pair of cells, narrowly conical in outline; slightly smaller flanking projections of similar shape, closely adpressed to the central projection, lying above the outer two thirds of each of the central cells, their outer margins more or less on a line with the septa dividing the central cells from their lateral companions. Behind the outermost fully enclosed cell on each side a further pair of small cells forming the front face of a raised eminence behind and lateral to the outer projections. Anterior lateral supplementary leaflet extending slightly on to the lip, at the level of the nostrils joined to a wart bearing a long tactile hair, then with a further short posterior extension; second leaflet not extending anteriorly quite so far, also joined to the central wart thus sharing it with the anterior leaflet, then extending posteriorly to form a part of the posterior leaf just above the eye, united to the rear wall of the semicircle of cells at the base of the posterior leaf; intermediate leaf and lateral eminences of posterior leaf furnished with long tactile hairs.

Ear most unusual; short, the anterior and posterior margins arising close together, nearly symmetrical, the anterior margin smoothly curved, the tip barely perceptible, the posterior margin similarly smoothly curved to give the appearance of a collar-like rim; ear membrane thickened at antitragal lobe; thumb minute; calcar short, about one quarter length of uropatagial margin; terminal tail vertebra scarcely projecting from membrane.

Skull very small and delicate; braincase relatively large, lacking lambdoid crests; a very slight anterior sagittal ridge; postorbital region markedly constricted. Rostrum short, low, weak and narrow, lacking supraorbital ridges, the lateral swellings little inflated; canine bearing part of maxilla slightly prolonged anteriorly; anteorbital region unusual in absence of anterior opening of anteorbital foramen, usually a pore-like opening posteriorly in anterior zygomatic root. Zygomata slender and strongly convergent anteriorly, wider posteriorly, with well-developed posterior jugal projection above glenoid, confined to posterior third of zygoma, extending posteriorly almost to its posterior root; anterior margin of projection gently and smoothly curved upwards to an acutely pointed and backwardly directed tip, the posterior margin obtuse, nearly straight, at extreme rear of zygoma. Premaxillae normal, anterior palatal foramina unenclosed, premaxillae making a V-shaped junction with the maxillae; palate short, terminating posteriorly just in advance of rear of m^{2-2} ; palation wide, U-shaped, with short, broad median spine; sphenoidal bridge narrow, not concealing lateral apertures; sphenoidal depression moderate, delimited laterally by well-defined divergent ridges extending from the base of the pterygoids to the antero-internal corners of the cochleae; sphenoidal apertures large; cochleae not expanded, in width about one and one half times their distance apart.

Dental formula $i\ 1/2$, $c\ 1/1$, $pm\ 2/2$, $m\ 3/3 = 30$, not $i\ 1/2$, $c\ 1/1$, $pm\ 1/2$, $m\ 3/3 = 28$ as implied by Miller (1907: 114). Upper incisor (i^2) bilobed, outer lobe slightly the larger; c^1 slender, narrow, with slight cingulum and small anterior basal cusp, stronger posterior cusp extending along about one third of the shaft; anterior upper premolar (pm^2) small, extruded, c^1 and second upper premolar (pm^4) in contact or nearly so; m^3 little reduced, with metacone and small fourth commissure, sometimes with fourth commissure nearly as long as third, terminating in a weak metastyle; i_{1-2} tricuspid, slightly imbricated; anterior lower premolar (pm_2) varying from about one third the crown area and one half the height of the second lower premolar (pm^4) to three quarters or more of its crown area and two thirds its height; m_3 not reduced, its posterior triangle slightly larger than the anterior triangle, with well-developed hypoconid and entoconid.

Humerus unusual among hipposiderids; trochiter a little smaller than trochin, projecting beyond ovate humeral head, separated from it by a moderate groove, the groove slightly deepened anteriorly to form a shallow supraglenoid fossa; ventral face of humeral head slightly hollowed; trochin strong, about level with head; no deltoid crest, the anterior face of humerus slightly flattened medially, a slightly raised area behind and below trochiter extending distally to edge of widened shaft; trochiter and trochin supported

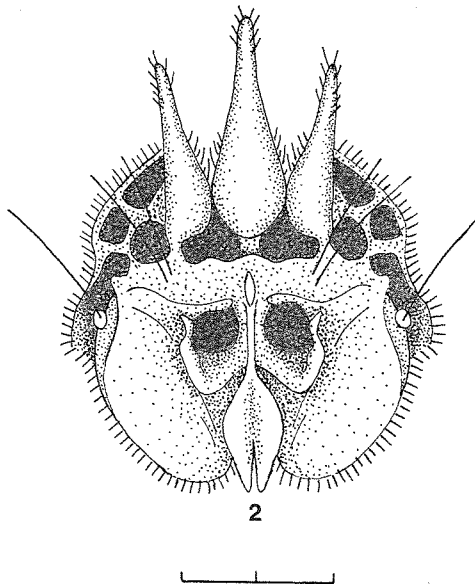


Fig. 2. *Cloeotis percivali*. BM(NH) 56.550. Anterior view of noseleaf. Scale = 2 mm.

by narrow dorsal and ventral flanges along sides of flattened proximal part of shaft. Capitellum slightly displaced from line of shaft, its principal articular surface wide, lateral surface and trochlea about one quarter to one third its width; epitrochlea small, narrow, about one third width of total distal articular surfaces, with strong distal process not separated from the trochlear rim of which it forms a part.

The genus is easily distinguished by its short, cropped ears and by the peculiarities of its noseleaf and skull. Although superficially it recalls *Rhino-nycteris* in the presence of a longitudinal process above the anterior leaf, the median projection of the intermediate leaf and the cellular construction of the base of the posterior leaf it differs sharply from this genus in numerous detailed aspects of its noseleaf and in a number of cranial and dental features. In the same way, the features of the noseleaf suggest *Triaenops* even more closely, but cranially the two genera are very distinct. *Cloetotis* also seems unusual in the structure of the proximal part of the humerus. The genus contains but one species, with a relatively restricted distribution in eastern and southern Africa.

***Cloetotis percivali* Thomas, 1901**

The species was reviewed in considerable detail by Hayman (1960: 167) who examined most of the extant material. Two subspecies are recognised, separated chiefly by size and by a minor feature of the dentition: orange and grey colorations are found and as suggested by Hayman & Hill (1971: 31), colour does not appear to be a reliable subspecific character.

***Cloetotis percivali percivali* Thomas, 1901**

Cloetotis percivali Thomas, 1901: 28. Takaunga, north of Mombasa, Kenya.

Slightly smaller; anterior lower premolar (pm₂) three quarters or more the crown area of the second lower premolar (pm₄) and more than one half its height. Measurements: length of forearm (2) 30.8–32.2; postorbital width (1) 1.6; c–m³ (1) 4.0. The holotype (BM[NH] 1.5.1.11) evidently has been damaged or has deteriorated since Thomas (1901: 30) obtained a wider range of measurements from it. These are: greatest length of skull 13; basal length 9.5; zygomatic width 7; width above orbits 3.3; width of interorbital constriction 1.8; mastoid width 6.5; front of canine to back of m³ 3.8. The subspecies is so far limited to Kenya: a specimen reported as *C. p. percivali* from Zimbabwe by Harrison (1959: 228) was thought more likely to be *C. p. australis* by Hayman (1960: 168), in which it is included by Smithers & Wilson (1979: 59).

***Cloetotis percivali australis* Roberts, 1917**

Cloetotis percivali australis Roberts, 1917: 264. Mooimeisjesfontein, Rustenburg, Transvaal, South Africa.

A little larger than *C. p. percivali*; anterior lower premolar (pm₂) one half or less the crown area of the second lower premolar (pm₄) and less than one half its height. Measurements: length of forearm (6) 32.5–34.5; greatest length of skull (5) 13.0–13.5; greatest length of skull to canine (5) 12.9–13.4; condylocanine length (5) 10.9–11.3; basal length (6) 9.8–10.3; width of rostrum above orbits (6) 3.2–3.4; postorbital width 1.6–1.8; zygomatic width (6) 7.1–7.6; width of braincase (6) 5.9–6.4; mastoid width (4) 6.9–7.2; c-m³ (6) 4.1–4.3; c-m₃ (6) 4.2–4.4. The subspecies is distributed from Zaire (Katanga) to Mozambique, Zambia, Zimbabwe, Botswana, South Africa (Transvaal) and Swaziland.

Genus *Triaenops* Dobson, 1871

Triaenops Dobson, 1871: 455. — *Triaenops persicus* Dobson, 1871.

Muzzle broad and rather flat; noseleaf narrow, not completely covering muzzle; lateral supplementary leaflets none or two, when absent a thick, fleshy ridge. Lateral margins of anterior leaf slightly indented at level of nostrils, anterior margin deeply emarginated, the edges of the emargination flexed upwards and sometimes recurved through almost their entire length to support and form part of a broad, flattened, longitudinal horizontal process extending medianly from the front of the internarial septum over the central part of the anterior leaf. Nostrils deeply pocketed with prominent narial lappets; intermediate leaf slightly swollen laterally with prominent, sharply pointed median projecting process. Posterior leaf complex, strongly cellular, its upper part tridentate, the projections long, pointed and prominent. Ear moderate, with definite point, anterior margin convex, sometimes emarginate, posterior margin straight or slightly concave distally, convex proximally, slightly thickened at the antitragal lobe and with prominent, thickened internal antitragal fold; calcar variable; tip of tail scarcely protruding from membrane.

Skull with elongate, rather narrow braincase, with slight lambdoid crests; sagittal crest and supraorbital ridges present; rostrum elevated, as high or nearly as high as braincase, the narial compartments inflated, separated medianly; anteorbital foramen rounded, separated by a narrow bar; zygoma with prominent, high jugal eminence; canine bearing part of maxilla not elongated or prolonged anteriorly. Premaxillae unusually thickened, with distinct median longitudinal ridge along their junction, the ridge slightly higher posteriorly and anteriorly raised into a low, blunt, upwardly directed point; premaxillae making a V-shaped junction with the maxillae, with delicate lateral processes that do not enclose the anterior palatal foramina; palation U-shaped, level with front of m²⁻²; sphenoidal bridge moderate, not obscuring lateral apertures; shallow sphenoidal depression; cochleae about three times as wide as their distance apart, or a little wider than this.

Dental formula $i\ 1/2, c\ 1/1, pm\ 2/2, m\ 3/3 = 30$. Upper incisor (i^2) bilobed, the outer lobe usually slightly the smaller; c^1 with slight external cingulum, a strong posterior secondary cusp extending along about one half the length of the shaft; anterior upper premolar (pm^2) small, extruded, c^1 and second upper premolar (pm^4) sometimes almost in contact; m^3 with metacone and trace of fourth commissure; i_1 bicuspid, slightly hollowed posteriorly, slightly smaller than i_2 which is tricuspid and a little thickened, the outer lobe the smallest, the central lobe by a little the largest; c_1 slender; anterior lower premolar (pm_2) ovate, squat, about two thirds the crown area but less than one half the height of the second lower premolar (pm_4); m_3 unreduced, its posterior triangle a little larger than its anterior triangle, with well developed hypoconid and entoconid.

Humerus with trochiter about as big or a little larger than trochin, extending considerably beyond humeral head, from which it is separated by a moderate to deep groove with anteriorly a moderate or deep supraglenoid fossa; trochin terminating level with humeral head, which is ovate and slanted, its ventral face hollowed. Deltoid crest displaced dorsally to lie behind trochiter, quite well developed to strong; ventral face of shaft with narrow flange beneath trochin. Capitellum only slightly displaced from line of shaft, its principal articular surface wide, lateral surface about one quarter width of principal surface; trochlea slightly wider than lateral surface; epitrochlea very small, about one third the width of the total articular surface, but with strong distal process, separated from the trochlear rim by a narrow space.

The genus *Triænops* is distributed from Iran through Arabia to much of eastern Africa, extending as far south as Mozambique; although for the most part not reported further west than Uganda it has been recorded from Loudima, in the Republic of the Congo, and almost on the west coast of the continent. It occurs also on Madagascar and on Aldabra, Picard and Cosmoledo islands, but specimens from these locations are uncommon and the classification of the genus on Madagascar must remain uncertain. Contributors to the taxonomy of *Triænops* include Tate (1941: 3), Dorst (1948: 15), who reviewed the genus in some detail, Harrison (1955: 900, 1963: 71, 1964: 105) and Aellen & Brosset (1968: 450). Currently, four species are recognised (Hayman & Hill, 1971: 30), one continental in distribution, the others confined to the Malagasy region. They are here reduced to two, albeit with some diffidence since it has not been possible to examine Madagascan material and to this extent the classification put forward must remain provisional.

There is a number of resemblances between *Triænops*, *Rhinonycteris* and *Cloeotis*. In some ways *Triænops* appears to link the other genera, or it may share features either with one or with the other, while in some respects it is independent. All have a median longitudinal horizontal process

lying over the anterior leaf: in *Rhinonycteris* it is more or less the shape of an hour glass, in *Cloeotis* cuneiform, forked anteriorly into two projections. In one species of *Triaenops* the process is similar to that of *Rhinonycteris*, in the other to that of *Cloeotis*. The posterior leaf in *Triaenops* is tridentate as in *Cloeotis* but the arrangement of its cells with a large median cell flanked laterally by smaller cells resembles *Rhinonycteris* rather than *Cloeotis* which has a band of cells encircling the upper part of the intermediate leaf. Only in *Triaenops* does there appear any structure for closing the opening of the large median cell, and then in one only of the two species. As in *Rhinonycteris* the anterior lateral secondary leaflet is represented in one of the species of *Triaenops* by a thickened fleshy ridge; in the other species of *Triaenops* there is a secondary leaflet partially encircling the muzzle, with a small second leaflet, a development in some respects further than that found in *Cloeotis*. The ears of *Triaenops*, although short, are less so than in *Cloeotis* and are pointed as are the longer ears of *Rhinonycteris*, yet in one species of *Triaenops* are developed further with an emargination in the anterior margin. Cranially, *Triaenops* differs from either of the related genera in its raised and inflated rostrum and relatively much larger cochleae, but resembles *Rhinonycteris* in the structure of the anteorbital region, the architecture of the jugal prominence of the zygoma and in its curiously thickened premaxillae. On the balance of characters, therefore, *Triaenops* apparently stands a little closer to the Australian *Rhinonycteris* than to the aberrant African genus *Cloeotis*.

The two species here recognised may be keyed:

Noseleaf with thickened supplementary ridge; median anterior process forked anteriorly; outer margins of lateral projections of posterior leaf basally smoothly convex; anterior margin of ear evenly rounded; rostrum with lateral profile of nares nearly vertical *T. furculus*

Noseleaf with two lateral supplementary leaflets; anterior margin of median anterior process linear or slightly concave; outer margins of lateral projections of posterior leaf basally emarginated; anterior margin of ear with central step-like emargination; rostrum with lateral profile of nares sloping posteriorly *T. persicus*

***Triaenops furculus* Trouessart, 1906**

Triaenops furcula Trouessart, 1906: 446. Grotto of Sarondrana, near Tulear, (St. Augustin Bay), west coast of Madagascar.

(?) *Triaenops aurita* Grandidier, 1912: 8, text-fig. Near Diego-Saurez, extreme northern Madagascar.

(?) *Triaenops furinea* Tate, 1941: 3. (?) Lapsus.

Noseleaf lacking lateral supplementary leaflets, instead surmounting a thick, fleshy ridge extending from the base of the posterior leaf completely

beneath the margin of the anterior leaf, with anteriorly a double fold or involution medianly; median longitudinal process above anterior leaf narrow posteriorly at base of internarial septum, widening quite abruptly, bifurcated over median emargination of anterior leaf to form two rather broad, pointed, anteriorly directed projections, these supported beneath for almost their entire length by the upturned margins of the emargination which form a part of the inner edges of the processes; posteriorly the process is raised laterally to give a gutter-like appearance. Median process of intermediate leaf laterally flattened, slightly upwardly directed; posterior leaf a complex of eleven cells or pits, five immediately surrounding the back of the intermediate leaf, their dividing septa thin, the outermost pair unenclosed basally, the median cell very large, almost as wide as the intermediate leaf, partially divided centrally by a low, incomplete septum. Median posterior projection large, acutely conical, its lateral margins slightly convex, its base one half as wide as the median cell, directly above the incomplete median septum; lateral projections slightly smaller, closely adpressed to the central projection, their outer margins convex to base, not basally emarginated, the septa dividing the median cell from its companions inserted at the base of the lateral projections, the outer margin of the projection extending ventrally to form the outermost wall of each companion cell; taken together the

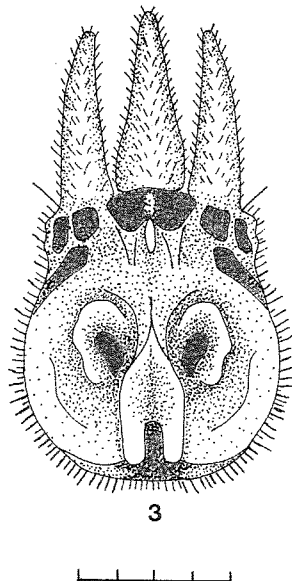


Fig. 3. *Triaenops furculus*. BM(NH) 78.185. Anterior view of noseleaf. Scale = 4 mm.

three projections extending across almost the entire width of the posterior leaf. A further pair of enclosed cells behind the lateral pair of cells on each side, the outermost visible anteriorly, the smaller inner cells lying behind the outer half of the base of each of the lateral projections, not visible frontally, their rear walls each supporting two fleshy eminences; beneath these, in front of the eye, an unenclosed, pit-like cell on each side.

Ear large, reaching to tip of muzzle when laid forward, its anterior margin smoothly convex, posterior margin straight distally, then convex; calcar a cartilaginous thickening, occupying about one quarter of the uropatagial margin.

Skull with sagittal crest commencing posteriorly over parietal suture, extending anteriorly over postorbital region just to rear of rostrum; posterior narial compartments much inflated, elevated, larger than anterior compartments which are rather small; very slight median rostral depression; anterior part of rostrum raised, its anterior profile nearly vertical; upper margin of narial opening lacking any broad, median spike; zygoma not thickened anteriorly, the zygomatic eminence extending over almost its entire length, its anterior margin slightly concave, its tip rounded and the posterior margin straight, the eminence about as high as a point level with the upper edge of the anteorbital foramen; i_1 bicuspid, not tricuspid as stated by Trouessart (1906: 447).

The species is known from Madagascar and from the islands of Aldabra, Picard and Cosmoledo, western Indian Ocean. There is little doubt that as Dorst (1947a: 308) suggested, it is the less specialised of *Triaenops*, certainly in the features of its nasal foliations. Although cranially rather characteristically of this genus, its noseleaf is less complex than in its congener, lacking any definite lateral supplementary leaflets but instead with a subsidiary fleshy ridge, with a less complex arrangement of fewer cells in the posterior leaf, and with the 'trident' wider, its individual projections perhaps less modified. The ears, too, seem less differentiated, lacking any step-like emargination in the anterior border. At the same time, however, the anterior horizontal process over the anterior leaf is modified with two small, parallel anterior projections, much as in *Cloeotis*. Apart from the features of the noseleaf it differs quite sharply from *T. persicus* in the structure of the rostrum, with its large, inflated posterior narial compartments and elevated anterior part: in *persicus* the posterior compartments, although inflated, are small, and the front of the rostrum is lower, in profile sloping down to the canines and not angular and nearly vertical as in *furculus*.

Triaenops aurita Grandidier, 1912. The description and illustration of *Triaenops aurita* suggest that it may be a synonym of *T. furcula*, as indeed it is generally listed. In particular Grandidier's emphasis on large ears indicates this species, but Dr. R. L. Peterson of the Royal Ontario Museum has sugges-

ted (pers. comm.) that *aurita* may be distinct. The holotype is apparently in poor condition.

Triaenops furinea Tate, 1941. This name derives from Tate (1941: 3) who lists „*Triaenops furinea* Trouessart“ from „Aldabra Islands“, without further description. Trouessart seems never to have described a species of this name (Aellen & Brosset, 1968: 450, footnote; Hill, 1971: 575) which may result from a mis-reading of *furcula*. Certainly a specimen from Aldabra was sent to Trouessart, who compared it with the holotype of *furcula* and confirmed its identification as that species (Fryer, 1911: 417).

***Triaenops persicus* Dobson, 1871**

Noseleaf with two lateral supplementary leaflets; edges of deep anterior emargination of anterior leaf flexed upwards and recurved to form an open sub-tubular structure beneath, supporting and part of the longitudinal horizontal process over the anterior leaf; this process more or less the shape of an hour glass, wide, rounded and occasionally distinctly bilobate posteriorly, then narrowed, its lateral margins concave for much of their length, the deepest part of the concavity a little towards the front of the process which widens abruptly into a short, broad anterior expansion, with its postero-lateral edges convexly rounded and usually slightly thickened, its anterior edge almost straight or slightly concave; posteriorly the edges of the process are slightly raised to give it at the back a gutter-like appearance. Intermediate leaf with prominent, lanceolate, sharply pointed median process, triangular in frontal outline, with strong median ridge extending to its tip.

Posterior leaf a complex of thirteen cells with medianly a deep central cell immediately behind the projecting process of the intermediate leaf, the opening of this cell closed by a fleshy prolongation of its lower edge directly posterior to the base of the projection and attached to the rear of its base by a low connective band; median cell separated from its companions by thick, fleshy septa: flanking this cell on each side a band of three deep cells separated by moderate septa, the lowermost open at the base, the second cell level with the central cell in the leaf, and the uppermost flanking the projections from the upper part of the leaf, its dorsal edge a base for two fleshy, wart-like elevations to the side of the lateral projections of the posterior leaf. Behind the lowermost pair of these cells two further enclosed cells on each side, the lower the larger, formed by the bifurcation of the anterior supplementary leaflet, behind this lower cell a further smaller cell, just in front of the eye. Central projection from the upper part of the posterior leaf the largest, proximally cylindrical, distally tapered to a point, its base forming the roof of the median central cell; lateral projections closely adpressed to central projection, smaller, their outer margins convex, basally with a strong concavity or emargination to provide a narrow insertion, the base of each lateral projec-

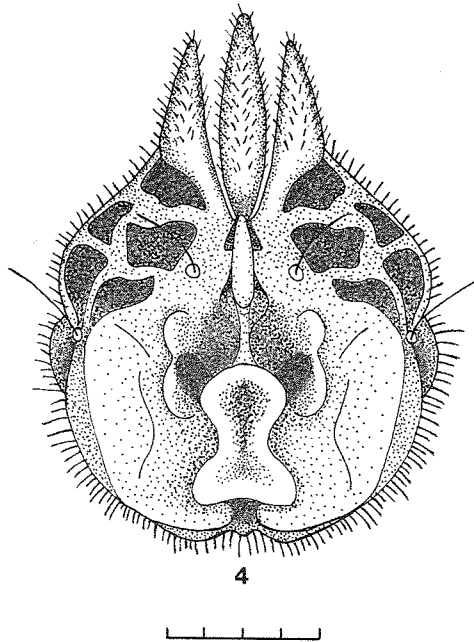


Fig. 4. *Triaenops persicus*. BM(NH) 72.4372. Anterior view of noseleaf. Scale = 4 mm.

tion a prolongation of the fleshy septum dividing the central cell from its lateral companions; taken together the total width of the three projections about one half the width of the posterior leaf.

Anterior lateral supplementary leaflet extending completely beneath anterior leaf, slightly emarginated medianly and with a downward median fold immediately under the sub-tubular structure beneath the horizontal median process of the anterior leaf; deeply and rather broadly emarginated anterolaterally, again emarginated at about the level of the nostrils to join a small wart, from this protuberance bifurcated posteriorly, the foremost prolongation the rear wall of the unenclosed cell at the base of the posterior leaf, the hindmost prolongation the rear wall of the small cell immediately behind it; second supplementary leaflet small, lappet-like, behind and slightly below bifurcation of anterior supplementary leaflet.

Ear short, broad, not reaching to tip of muzzle when laid forward, with definite point; anterior margin convex, with prominent step-like emargination a little more than halfway along its length, rising to relatively narrow, rather acute point, posterior margin slightly concave behind tip, then smoothly and fully convex; a small bony process originating from the proximal extremity

of the second phalanx of the fourth digit, enclosed in the wing membrane, directed outwards, obtusely pointed; calcar extending along a little less than half of the uropatagial margin.

Skull with well developed sagittal crest extending from occiput just to supraorbital region where it merges into very slight supraorbital ridges; rostrum elevated posteriorly, the posterior narial compartments inflated but small, anterior narial compartments much larger; a shallow median rostral trough, posteriorly slightly deepened to form a shallow depression; lateral rostral profile sloping to canine; upper margin of narial opening with a short, broad, anteriorly directed median spike; zygoma widened anteriorly, zygomatic eminence large, well developed and rounded, its anterior edge smoothly convex, its posterior edge more abruptly so, inserted almost at squamosal, the eminence about as high as upper insertion of anteorbital bar.

The species is distributed from eastern Iran, Oman and Aden through eastern Africa to Zimbabwe, Mozambique and Madagascar: it has been found in the Republic of the Congo, but a present there is a wide geographical hiatus in its distribution in central Africa, there being no other reports west of Uganda. Currently three subspecies are recognised, separated by small differences in coloration and size. These have been increased to four in the present study by the suggested addition of the Madagascan form *rufus*, with its compatriot *humbloti* as a possible synonym, these having been listed as distinct species by Hayman & Hill (1971: 30), *humbloti* admittedly with some reservation. Like many other hipposiderids, the species is encountered in two distinct colorations, in this case one more or less pale greyish brown dorsally with buffy underparts, the other brighter with the back and sometimes browner underside tinged with red or orange.

***Triaenops persicus persicus* Dobson, 1871**

Triaenops persicus Dobson, 1871: 455, pl. 18. Shiraz, Fars Province, Iran.

Triaenops persicus macdonaldi Harrison, 1955: 900. Al Ain, Buraimi Oasis, Oman.

The only specimens (one a 'cotype') of *T. p. persicus* available in the British Museum (Natural History) have been in alcohol for many years and are therefore of little value for colour comparison. However, Dobson (1871: 457) says "On the upper surface the fur is very pale buff, almost white, with light sepia tips, darkest on the back of the neck, along the anterior margin of the scapulae, and between the shoulders; towards the root of the tail of a yellowish tinge throughout; beneath; wholly very pale buff or dirty yellowish white ...". Detailed accounts of colour and colour variation in this subspecies have also been provided by DeBlase (1978: 111, 1980: 130), who found that the palest individuals of a series of specimens matched the description by Dobson, being similarly slightly darker in the shoulder and head regions,

Table 1. Measurements of *Triaenops*

	Number of specimens	Length of forearm	Number of specimens	Condylacanine length	Number of specimens	c-m ³
<i>T. lurculus</i>	3	43.0-45.1	1	15.0	3	6.2-6.4
<i>T. persicus persicus</i>						
Iran	2	51.3-51.9	2	16.0-17.3	2	6.6-7.0
Oman (<i>macdonaldi</i>)	15	45.9-52.0	15	15.5-16.9	15	6.9-7.3
<i>T. persicus afer</i>						
Aden	5	52.9-54.9	4	16.9-17.8	4	7.1-7.3
Somalia	6	50.4-54.3	5	15.4-17.4	6	6.2-7.3
Ethiopia	19	50.8-55.8	1	15.8	1	6.2
Kenya	4	52.0-55.2	1	16.9	2	6.8-6.9
Tanzania	25	51.7-56.1				
Zanzibar	2	50.4-52.7	2	15.4-15.5	2	6.2-6.3
<i>T. persicus majusculus</i>						
Uganda	14	53.1-57.7				
Republic of the Congo*	9	53.4-60.1	4	16.4-17.8	7	6.6-7.5
<i>T. persicus (?) rufus</i>						
Madagascar**	6	51-55				
Madagascar (<i>humbloti</i>)**	6	50-54				

* From Aellen & Brosset (1968: 452). The large specimen with forearm 60.1 seems exceptional: the mean of the series is 55 (loc. cit., p. 451) and without this example the range is 53.4-57.5.

** From Dorst (1948: 21)

but lacking the yellowish tinge towards the root of the tail. The series also included specimens with darker, browner dorsal pelage, the ventral surface sometimes with a slightly reddish tinge, one such darker example with pale buff underparts closely resembling the holotype of the allegedly darker subspecies *T. p. macdonaldi*, a final specimen having a strong reddish tinge in the pelage, especially ventrally. It should be noted that among measurements given by DeBlase (1978: 115, tab. 14, 1980: 389, 390) the values for the breadth of the braincase (BB) in BM (NH) 76.3.10.3 and BM(NH) 97.11.10.1 re-

fer in fact to the mastoid width (or mastoid breadth, MB). The correct values for the breadth or width of the braincase in these specimens are 7.3 and 7.9 respectively.

Triaenops persicus macdonaldi Harrison, 1955. This subspecies was separated from *T. p. persicus* on the basis of darker colour and possibly smaller cranial size when compared with the two Iranian examples in the British Museum (Natural History) and with Dobson's original description. The majority of the original series is light greyish brown dorsally, the ventral surface olive brown to cream buff; one example is dorsally light brown, with darker, ochraceous buff face, crown and throat, its ventral surface otherwise cream buff, slightly orange. Further examples from Oman in the Harrison Zoological Museum, Sevenoaks, Kent, England agree closely with the original material. DeBlase (1978: 116, 1980: 131) has concluded from an examination of a series of Iranian specimens of *T. p. persicus* and of the holotype of *macdonaldi* (now BM(NH) 67.1227) that the subspecies cannot be maintained either on colour or on size.

Colour is clearly variable and may well be unreliable as a diagnostic character, while measurements given by DeBlase (1978: 114, 1980: 131) for the skull of the holotype of *macdonaldi* fall within the range that he gives (1978: 115, tab. 14, 1980: 389, 390) for *T. p. persicus* from Iran, although his breadth of the braincase (BB) for this skull clearly refers to its mastoid width (= mastoid breadth, MB), the breadth or width of its braincase in fact being 7.5. Further examination confirms DeBlase's remaining measurements, which considerably exceed corresponding values given by Harrison (1955: 903, 1964: 104) for this specimen and indeed those provided by this author for the original series of *macdonaldi*. However, the measurements of the original material by Harrison (loc. cit.) are consistently low when compared with recent measurements of the same specimens. For example, the condylobasal length is given as 16.2–17.2 but more correctly is 16.5–17.6, the zygomatic width as 8.0–8.7 but is instead 8.3–8.9, and the length of the maxillary tooth-row ($c-m^3$) appears as 6.3–6.6 rather than 6.6–7.0. In fact, these and other examples obtained more recently in Oman agree closely in cranial size with those of *T. p. persicus* from Iran reported by DeBlase (loc. cit.). A small individual recorded from Ibri by Atallah & Harrison (1967: 313) is the smallest of the series: the Harrison Zoological Museum includes a second, much larger specimen from the same location.

The subspecies is known in Iran from Nikshahr in the Sistan and Baluchistan Province (DeBlase, 1980: 129), from Shiraz in Fars Province and from Bushehr (= Bushire) and Ahram (Lay, 1967: 139) in Bushehr Province. As *macdonaldi* it has been reported in Oman from Al Ain and Ibri, from Uhi and Sohar (Harrison, 1972: 627), and there are further specimens in the Harrison Zoological Museum from Hazm Fort, near Rostaq.

***Triaenops persicus afer* Peters, 1877**

Triaenops afer Peters, 1877: 913, fig. 2. Mombasa, Kenya.

Darker than *T. p. persicus*, some examples dorsally brownish with little or no grey and ventrally greyish buff, others more reddish brown dorsally, the ventral surface similar in colour but slightly paler.

This form was long considered specifically distinct from *T. persicus*, Dorst (1948: 18, 20) for example using as a diagnostic character the structure of the median projection of the intermediate leaf which he believed divided at its tip into two points in *afer* but to have only a single point in *persicus*. However, this feature is variable (Aellen & Brosset, 1968: 450) and Harrison (1964: 105) was unable to find any characters of specific value between the two, referring specimens from Aden to *T. persicus afer*.

The subspecies is distributed from Aden through Somalia, Ethiopia, Kenya and Tanzania to Zimbabwe (Smithers & Lobão Tello, 1976: 74, Smithers & Wilson, 1979: 60) and Mozambique. Hayman & Hill (1971: 30) queried its occurrence on Zanzibar but the collections of the British Museum (Natural History) include specimens from that island.

***Triaenops persicus majusculus* Aellen & Brosset, 1968**

Triaenops persicus majusculus Aellen & Brosset, 1968: 450. Doumboula Grotto, Lou-dima, Republic of the Congo.

This subspecies is very similar to *T. p. afer* but is very slightly larger. It has been known hitherto only from the type locality but Ugandan specimens also appear referable to it: a series (BM(NH) 65.138-151) from a locality 7 miles S of Moyo, West Madi County, West Nile District is intermediate in size between *T. p. afer* and *T. p. majusculus* but tends towards the latter.

***Triaenops persicus* (?) *rufus* Milne Edwards, 1881**

Triaenops rufus Milne Edwards, 1881: 1035. East coast of Madagascar.

(?) *Triaenops humbloti* Milne Edwards, 1881: 1035. East coast of Madagascar.

No specimens referable either to *rufus* or to *humbloti* have been examined. However, the type material of both is in the Muséum National d'Histoire Naturelle, Paris and has been described and commented upon by Dorst (1947a: 309, 1948: 20, 21). According to this author (1948: 21), the narial foliations of *rufus* are much as in *T. p. afer* but the median projection of the intermediate leaf has a single point, an unreliable character (vide supra), and the median longitudinal projection over the anterior leaf is shorter, with smooth, less abrupt emarginations in its lateral edges, situated at the centre of the edge rather than at the rear of its anterior third (loc. cit., p. 16, fig. 1). However, the emarginations in the lateral edges of the process in some specimens of *T. p. afer* are more centrally than anteriorly placed and more-

over the posterior margin of the process is also variable, being quite definitely a little bilobed in some examples, or smoothly rounded in others. It is clear from the illustrations of the head and noseleaf of the holotype of *rufus* by Dorst (1948: 20, fig. 3) and of the longitudinal process (loc. cit., p. 16, fig. 1 b), together with the earlier drawings of the head and leaf by the same author (1947b: 84, fig. 6) and posterior leaf (loc. cit., p. 85, fig. 7) that *rufus* is very near to *T. persicus* in the structure of its narial foliations, and it is considered here as a provisional subspecies of this widespread mainland species. It has been reported only from Madagascar.

Triaenops humbloti Milne Edwards, 1881. There seems every possibility that *humbloti* has been applied to paler examples of the species, *rufus* to more reddish specimens, these differing from each other chiefly in colour (Dorst, 1947a: 309, 1948: 20, 21), *humbloti* having greyish beige pelage both dorsally and ventrally, *rufus* reddish yellow on the back, paler beneath.

Summary

The major taxonomic features of three hipposiderid genera, *Rhinonycteris*, *Cloeotis* and *Triaenops* are described and discussed. Where appropriate, species and subspecies are diagnosed and defined, with an indication of geographic variation.

Zusammenfassung

Die wichtigsten taxonomischen Merkmale dreier hipposiderider Gattungen, *Rhinonycteris*, *Cloeotis* und *Triaenops*, werden beschrieben und diskutiert. Wo möglich, werden Arten und Unterarten diagnostiziert und definiert und Hinweise auf geographische Variation gegeben.

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