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Pinocchio lizards and other lizards bearing rostral appendages – the peculiar habitus of the draconine agamid *Harpesaurus tricinctus* with highlights on its ecological implications and convergence with its New World equivalent, the dactyloid *Anolis proboscis*

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Abstract. *Harpesaurus tricinctus* is an Asian agamid lizard described in 1851 from Java, Indonesia, and since then known only from its holotype located at the Paris Natural History Museum (MNHN-RA), supposedly a male, characterized by a long sickle-shaped rostral appendage. Ecological data are virtually lacking since no other specimen have ever been found. Here we review its morphology as compared with its congeners. We also review the morphology of other lizards and some snakes with rostral appendages and discuss their possible functional implications. We identified a South American dactyloid lizard, *Anolis proboscis*, the males of which show by their general habitus and a long, sword-shaped rostral appendage a striking convergence with the possibly extinct *H. tricinctus*. *Anolis proboscis* was also for long considered a rare and little-known lizard but recent field work allowing new observations provided additional data on its ecology. We suggest to use these new data on its habitat requirements which might be comparable to those of the externally so similar but allegedly extinct Indonesian agamid which might have survived in the canopy of tropical humid forests in one of the Greater Sunda Islands of Indonesia.

Key words. Squamata, rostral appendage-bearing (Pinocchio) lizards, convergent evolution, functional implications, tropical rain forest, arboreality.

Introduction

Head ornamentation, here the presence of rostral or supraorbital protuberances, is present in numerous animal groups. In avian reptiles, such bony structures like those seen in some bird groups, e.g. the rhinoceros birds (Bucerotidae), have a wide range of elaborate bony structures surmounting the prominent bill with different shapes and colors (Kemp 1995). Various theories suggested functions for the casques of hornbill. Some investigations even attributed a possible acoustic function for that casque structure (Alexander et al. 1994). Rostral and supraorbital outgrowths are also present in anuran amphibians as well as in squamate reptiles. In frogs of the families Megophryidae and Cyclorhamphidae for instance, it has, according to Cruz et al. (2010) and Munir et al. (2018), a somatolytic camouflaging function, but some species of the pelodryadid genus *Litoria* Tschudi, 1838 have sexually

dimorphic fleshy spikes at their snout tips which are interpreted as partly somatolytic and partly also responsible for mate recognition (Menzies & Johnston 2015, Oliver et al. 2019a, b). Also in squamates, rostral appendages can play a role in camouflaging, or, particularly when confined to males only, can have a function in sex-specific species recognition, thus being sexually selective (Ord & Stuart-Fox 2005).

In this paper, we focus on rostral appendages in lizards while nasal appendages are rarely observed in snakes. Apart from some viperids, such appendages (not only specialized rostral shields) occur in the Neotropical *Philodryas baroni* Berg, 1895 (Dipsadidae), as well as in the Oriental *Gonyosoma boulengeri* (Mocquard, 1897) and *G. hainanense* Peng, Zhang, Huang, Burbrink & Wang, 2021 (Colubridae) as well as in some vine snakes (Colubridae), particularly prominent in *Ahaetulla pulverulenta* (A. M. C. Duméril, Bibron & A. H. A. Duméril, 1854), but also devel-

oped to a lower degree in other congeners, e.g. *A. anomala* (Annandale, 1906), *A. laudankia* Deepak, Narayanan, Dutta & Mohapatra, 2019, *A. oxyrhyncha* (Bell, 1825) or *A. sahyadrensis* Mallik, Achyuthan, Ganesh, Pal, Vijayakumar & Shanker, 2019. Rare cases are the paired antenna-like rostral appendages in the homalopsid snake *Erpeton tentaculatum* Lacépède, 1800 which serve as sensitive mechanoreceptors under water (Winokur 1977, Fox 1999, Catania et al. 2010), or the acutely pointed rostral scale in the male sea snake *Emydocephalus annulatus* Krefft, 1869 and congeners used to stimulate the female during copulation (Hahn 1973, Guinea 1996, Fox 1999). A special case is the Malagasy pseudoxyrhophid genus *Langaha* Bonnaterre, 1790 (Guibé 1948, 1949), bearing a long even sexually dimorphic, leaf-like nasal appendage whose function is still not yet fully understood (Krysko 2005, Tingle 2012).

Apart from pathological nasal protuberances (e.g. Martinez-Silvestre et al. 1981 for a lacertid lizard), the elongated paired, funnel-shaped nasal scalation of the gekkonid *Rhinogekko misonnei* (de Witte, 1973) (Moradi et al. 2011) and the nasal protuberance of the male gharial *Gavialis gangeticus* (Gmelin, 1789) (Biswas et al. 1978) are mentioned here just for completeness' sake. In lizards, rostral appendages or protuberances are confined to the iguanian families (Iguanidae sensu lato, Agamidae and Chamaeleonidae) which will be discussed in more detail below.

A particular wide variety in head ornamentation and appendages can be found among Asian agamid lizards (Schulte et al. 2002, Ord & Stuart-Fox 2005). The herpetological collection of the National Museum of Natural History in Paris (MNHN-RA) houses a unique specimen of a bizarre Asiatic draconine lizard bearing a long, falciform (sickle-shaped) rostral appendage (Fig. 1). The lizard was described in a new genus as *Arpephorus tricinctus* A. H. A. Duméril, 1851 (*Arpephorus* being preoccupied by a beetle and replaced by *Harpesaurus* Boulenger, 1885). This is the only known specimen, and because the species has never been found again since its description (A. H. A. Duméril in A. M. C. Duméril & A. H. A. Duméril, 1851), it is re-garded as likely extinct. The five other species of the genus *Harpesaurus*, viz. *H. beccarii* (Doria, 1888), *H. borneensis* (Mertens, 1924), *H. brooksi* (Parker, 1924), *H. ensicauda* F. Werner, 1913, and *H. modiglianii* Vinciguerra, 1933 are all known from just a very few specimens. With the exception of *H. borneensis* (Lardner et al. 2010, Manthey 2010), their ecology remains a mystery. The allocation of the nomen *brooksi,* described in a new monotypic genus as *Thaumatorhynchus brooksi* to *Harpesaurus* was proposed already by Vinciguerra (1933) who was followed by Wermuth (1967), King (1978), Lardner et al. (2010), Manthey (2010), and Uetz et al. (2021). Only Moody (1980) suspected a closer affinity to the genus *Aphaniotis*.

We here compare this unique and only known specimen of *H. tricinctus* with all other lizards bearing a rostral appendage (mostly only in males) and show that one lizard species from a distinct, geographically remote, but likewise iguanian family (Dactyloidae), viz. *Anolis proboscis* Peters & Orcés, 1956, shows a striking convergence in habitus and color pattern. Such a spectacular convergence between a Neotropical iguanid and an Asian agamid in perch use and limb lengths had been already indicated for the Caribbean *Anolis* Fitzinger, 1843 and the Southeast Asian flying agamid *Draco* Linnaeus, 1758 by Ord & Klomp (2014). In both genera interspecific competition shaped ecobehavioral and morphological differentiation. There are numerous cases of such morphologically similar species "pairs" among iguanian families living on separate continents, e.g. the lizard genera *Sauromalus* A. H. A. Duméril, 1856 (Iguanidae) and *Uromastyx* Merrem, 1820 (Agamidae), *Basiliscus* Laurenti, 1768 (Iguanidae) and *Hydrosaurus* Kaup, 1828 (Agamidae), or *Phrynosoma* Wiegmann, 1828 (Phrynosomatidae) and *Moloch* Gray, 1841 (Agamidae). Almost a textbook example among snakes, the impressive convergence of the Neotropical *Corallus caninus* (Linnaeus, 1758) (Boidae) and Australo-Melanesian *Morelia viridis* (Schlegel, 1872) (Pythonidae) (Esquerré & Keogh 2016). All these examples show great similarities in their convergent habitat selection (see also Pelegrin et al. 2021).

Figure 1. *Harpesaurus tricinctus* in color. Reproduction of the holotype on vellum (MNHN vellum collection).

Since ecological data on other species of *Harpesaurus* are scarce or even completely missing (see below), we suggest to use the available data on the ecology of *A. proboscis* to provide inferences on habitats in which a rediscovery of *H. tricinctus* in Indonesia nearly 17 decades after its description might be more likely or even possible.

Results and Discussion
History of the unique *Harpesaurus tricinctus* specimen

In the "Catalogue Méthodique de la Collection des Reptiles", A. H. A. Duméril in A. M. C. Duméril & A. H. A. Duméril (1851: 92–93) described the monotypic new agamid genus *Arpephorus* characterized by its long rostral sickle-shaped appendage that reminded him of the form of a harp (Latin *arpe* = harp) and by a distinct tympanum whereas the genera *Ceratophora* Gray, 1834 and *Lyriocephalus* Merrem, 1820, likewise equipped with nasal protuberances, have a hidden tympanum. The unique specimen, holotype by monotypy, which is credited as having been collected on Java, is described as a new species, *Arpephorus tricinctus*, based on the three broad, light yellowish bands on its back. In a second paper which A. H. A. Duméril (1851) published alone, he indicated that he previously provided the diagnosis of his new genus *Arpephorus* in the "Catalogue Méthodique" published in April 1851 (A. M. C. Duméril & A. H. A. Duméril 1851), thus approving that the first-cited publication from the same year was actually earlier. A. H. A. Duméril (1851), redescribing both the genus and species a second time, stated that the unique available specimen was acquired several years earlier (no precise date indicated) as originating from Java and that it was present in the Muséum national d'Histoire naturelle (Paris) collections (MNHN-RA 0623 [former tag number 2020]); it was discovered desiccated and pinned dry in a box with insects [the hole made by the pin is visible on the back of the lizard; Fig. 2]. Note that in a recent checklist on amphibians and reptiles of Java and Bali, Kusrini et al. (2021) erroneously located that holotype at the Natural History Museum in London (UK). No collector name was indicated and none could be found in any of the MNHN-RA catalogues. Further no indication of any such lizard collected from Java (even without collector name) prior to 1851 was found in any available MNHN catalogues that we have checked (handwritten fish & reptile catalogues 1832–1838, 1839–1863; handwritten reptile gifts catalogue 1839–1864). Additionally, both handwritten 1857 and 1864 catalogues indicated "Java" as the location for the lizard and the later catalogue also said that an illustration on vellum had been made to illustrate the species (see Fig. 1; MNHN vellum collection). This lizard was designed and painted by Marie-Firmin Bocourt (1819–1904). It is "arranged" with two other colored drawings of Bocourt among the MNHN vellums, Portfolio 87, No. 99. This is the same drawing used by the engraver L. Lebrun to make the plate VII illustrating the original publication.

As *Arpephorus* A. H. A. Duméril, 1851 was preoccupied by *Arpephorus* Stephens, 1829 (Coleoptera), a new genus, *Harpesaurus* Boulenger, 1885, was created to accommodate the species previously referred to the former genus (Boulenger 1885). The genus *Harpesaurus* is characterized by its tympanum concealed by a scaly plate (in the type-species *H. tricinctus* and *H. borneensis* but not in other species generally included in the genus) and a snout ending in a long sometimes compressed (round in cross section in *H. brooksi*), cutaneous (not scaly) appendage. Body and tail are compressed, covered above with equal smooth scale of moderate size while ventral and tail scales are keeled. Except in *H. ensicauda* which lacks a dorsal crest, a more or less developed dorsal crest is often present on back and tail. No gular sac, no transverse gular fold, nor femoral or preanal pores are present (modified after Boulenger 1885).

Boulenger (1885) gave the following diagnosis for *H. tricinctus*: "Elongated rostral appendage longer than the head, formed of a unique compressed falciform scale curved upwards, surrounded at the base by a few large scales. Upper head-scales small, slightly tubercular; a large prominent triangular scale on the snout; canthus rostralis forming a serrated ridge. Gular scales tubercular. Dorsal crest a low serrated ridge. Dorsal scales smooth, equal, forming regular transverse series; ventral scales keeled. Scales on the limbs keeled. Tail transversely compressed, crested above, the crest a little higher than the dorsal; caudal scales keeled, the inferior spinose. Brown, with three broad transverse yellow bands on the body, the anterior narrowest on the scapular region". Snout–vent length of the unique known specimen (holotype by monotypy) is 168 and 166 mm and

Figure 2. Detail of the back of the holotype of *H. tricinctus* showing the black hole where the insect pin passed to conserve the dried lizard before it was discovered.

tail length 83 and 82 mm according to Boulenger (1885) and Brygoo (1988), respectively (Fig. 3).

Since its description in 1851, the species has never been found again. Moreover, its alleged geographic origin from Java cannot be confirmed since no collector name is associated with the specimen. The reproductive mode of *H. tricinctus* cannot be verified; although oviparity is most common among Asiatic draconine agamids, viviparity is known only from the two species of the Sri Lankan endemic genus *Cophotis* Peters, 1861, viz. *C. ceylanica* Peters, 1861 and *C. dumbara* Samarawickrama, Ranawana, Rajapaksha, Ananjeva, Orlov, Ranasinghe & Samarawickrama, 2006 (Samarawickrama et al. 2006, Manamendra-Arachchi et al. 2006, see Hallermann & Böhme 2007), and in one of the congeners of *H. tricinctus*, viz. *H. borneensis* (Lardner et al. 2010, Manthey 2010, Kurita et al. 2020).

The other species of *Harpesaurus*

The genus *Harpesaurus* as recognized today comprises six species confined to the Greater Sunda Islands. Next to *H. tricinctus* (likely originating from Java) these are: *H. beccarii* from Sumatra, *H. borneensis* from Borneo (Sarawak and Kalimantan), *H. brooksi* from Sumatra, *H. ensicauda* from Nias (Mentawai archipelago), and *H. modiglianii* again from Sumatra. All of them are known by a small number of individuals only, in one of them (*H. ensicauda*) even the single type specimen is lost, and ecological data, if any, are extremely scarce. So, nearly all these species belong to the group of "extinct, obscure or imaginary lizard species" as recently defined by Meiri et al. (2018). We rapidly indicate their main characters below:

Harpesaurus beccarii is characterized by a double rostral appendage in the male, viz. a lower median recurved one, and a second straight process above it. It is bright green in life with two short white, oblique stripes on the side of head and neck. Its body is laterally compressed and has separate nuchal and dorsal crests composed of large triangular scales; the caudal crest composed of lanceolate scales is separated from the dorsal crest. The strongly compressed tail forms in its first half a little sail supported by elongated neural spines of the proximal tail vertebrae. The rough drawing reproduced from Doria (1888) by de Rooij (1915) is rather imprecise in respect to all these characters. Photographs of a living male can be found in Böhme (1989) and Manthey (2010), both showing the same individual.
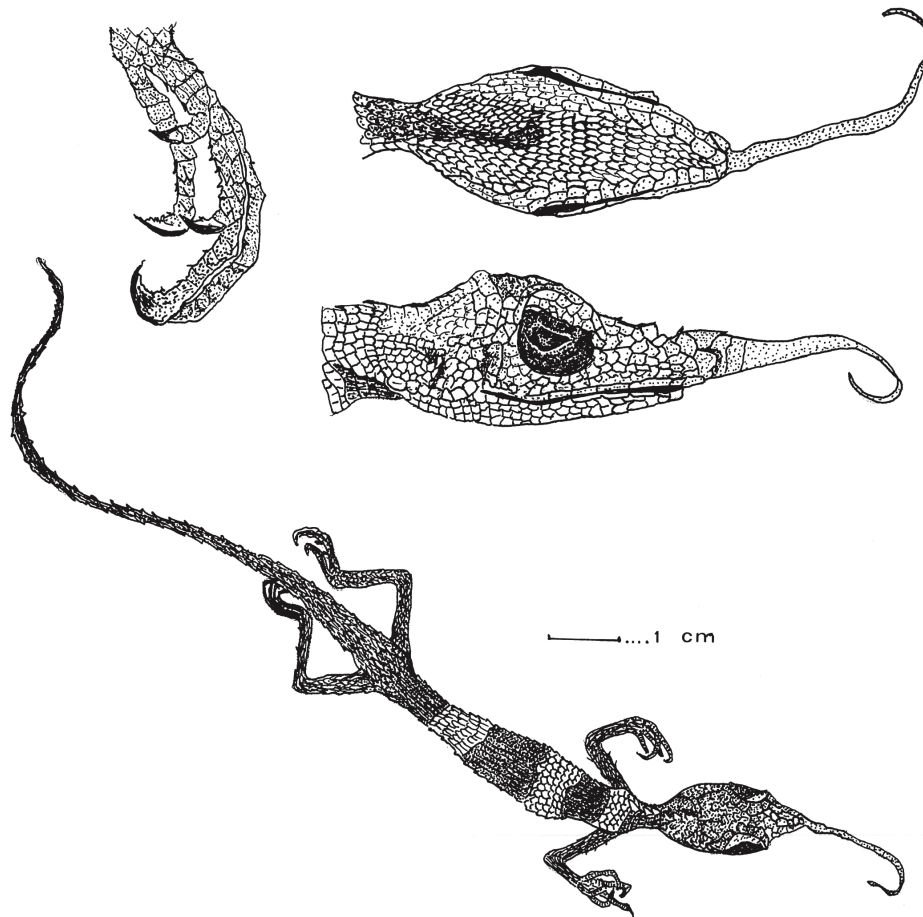

Figure 3. Holotype of *Harpesaurus tricinctus* (MNHN-RA 0623), drawing from Brygoo (1988: 49).

Harpesaurus borneensis was originally described as the only species of a monotypic genus *Hylagama* Mertens, 1924, based on a single female specimen. While Wermuth (1967) and Moody (1980) maintained this generic allocation, Manthey (2010) considered *Hylagama* as a synonym of *Harpesaurus*. King's (1978) new species *Harpesaurus thelescorhinus* was believed to be identical with Mertens' (1924) species (Moody 1980, Lardner et al. 2010, Manthey 2010). According to the drawing of the type specimens given by King (1978), the male holotype of his new species had a very long cylindrical (not compressed) curved rostral appendage, exceeding the head length, while the female paratype was hornless. Lardner et al. (2010) re-examined King's two type specimens deposited in the Chicago Natural History Museum (CNHM = FMNH). The male holotype proved to have a much smaller rostral appendage, reaching just the eye when laid backwards, while the female was hornless, as is also Mertens' (1924) female holotype of his *H. borneensis*. However, Lardner et al. (2010) were able to discover more females in Sarawak which had also (though much shorter) rostral appendages. So, the presence or absence of rostral appendages is either variable in this species or casts doubt on their conspecifity as ongoing examination will check (Denzer et al. 2021). Moreover, two of these females were found to be highly gravid with two rather large, well-developed fetuses each. More ecological data were provided by Kurita et al. (2020).

Harpesaurus brooksi was originally described as the sole representative of a new genus *Thaumatorhynchus* erected by Parker (1924), the synonymy of which with *Harpesaurus* was claimed by Vinciguerra (1933), Wermuth (1967), King (1978) and Manthey (2010). It is the second (of three) Sumatran species of *Harpesaurus,* characterized by a cylindrical rather than laterally compressed rostral appendage, a small dorsal and no caudal crest.

Harpesaurus ensicauda has no broad bands on the body but its tail is strongly compressed with a crest above (Werner 1913, de Rooij 1915). It is only known from its male holotype (Werner 1913, Wermuth 1967) which is today obviously lost. The only morphological characterization is that of Werner (1913) himself, referred to by de Rooij (1915). Its rostral appendage is shorter than the head, curved backwards and surrounded at the base by two enlarged scales. It has no dorsal crest, but a strongly compressed tail with denticulate projections on its upper margin.

Harpesaurus modiglianii, originally also known only from its single holotype collected in 1891, has recently been rediscovered by Putra et al. (2020) after 129 years. They recorded the find of two male specimens not far from the type locality in northern Sumatra, one encountered dead on the forest floor, and another one alive, which was released after photography. Both males agreed well with the type specimen in having also a single rostral appendage.

Three characters make *H. tricinctus* unique within this rather diverse genus, the monophyly of which has still to be demonstrated (Denzer et al. in prep.): (1) its tympanum is hidden by a scaly plate (like in *H. borneensis*), (2) no other agamid species has such an extended proboscis-like rostral appendage and also (3) none possesses its typical threefold banded black and yellow body pattern.

Other rostral appendage-bearing Iguania

Rostral appendages occur across the entire clade of iguanian lizards, particularly in many species of African and Malagasy chameleons, ranging from broad, flat, single or double scale-covered lobes to as many as six pointed, annulated horns on the snout tip. These rostral projections, sometimes forming annulated horns which can be combined with likewise annulated preorbital horns, are either used as visual signals, sometimes also as weapons in agonistic male contests on tree branches (Emlen 2008, Johnson et al. 2013, Stuart-Fox 2014), or as cues for sexual recognition (Rand 1961, Parcher 1971, Böhme & Klaver 1981), functions which will be discussed below.

Rostral appendages are moreover present in several other Asiatic agamids and some Neotropical iguanians. In the former they are considerably more variable in shape, number and squamation than those of the few proboscis-bearing anoles (Williams 1979).

Other agamid lizards with rostral appendage

Also, the small tree-dwelling draconine agamids of the Sumatran genus *Aphaniotis* Peters, 1864 have two species with rostral appendages in males: *A. acutirostris* Modigliani, 1889 and an undescribed species from the Mentawai Islands southwest of Sumatra, *Aphaniotis* sp. (de Rooij 1915, Lawalata 2011). The appendages are small, scaly structures.

There is another small draconine agamid lizard from Sumatra (?) and Java, where the males have also a rostral appendage which is, however, very tiny and not comparable with those found in the genus *Harpesaurus* or in the Sri Lankan draconine radiation dealt with below. It is *Pseudocophotis sumatrana* (Hubrecht, 1879) a likewise extremely rare arboreal lizard originally assigned to the genus *Cophotis*. A rather good line drawing of the male holotype from Leiden collections is given by de Rooij (1915). Another male specimen stored at the Senckenberg Museum in Frankfurt/Main (SMF 9741, former SMF 4276a) is reported by Mertens (1921) and figured in Hallermann & Böhme (2000). There are also two females known. The minute rostral appendage looks like a rudiment and has likely no functional meaning in an ecological or behavioral context. A further male specimen was recently recovered by Denzer et al. (2021).

One Asiatic draconine agamid clade (Kurita et al. 2020) endemic to Sri Lanka includes two lineages where the members have rostral appendages. One is *Lyriocephalus scutatus* (Linnaeus, 1758), with a knob-like rostral appendage, neither comparable to that of *H. tricinctus* nor to any other rostral appendage-bearing lizard. *L. scuta-*

tus is an oviparous arboreal species with a round, bulbous scale complex forming its rostral appendage (Schulte et al. 2002). It has a developed gular sac (similar to anoline throat fans), orange-yellowish in life, whereas its back is green with bluish flanks, and more prominent in the male which also possesses a nuchal hump. It is found in well-shaded natural forests and plantations (less in home gardens) in the wet and intermediate zones below 900 m a.s.l. (Karunarathna & Amarasinghe 2013).

The second lineage of this clade endemic to Sri Lanka is *Ceratophora* Gray, 1835, composed of six oviparous species lacking dorsal crests. They are characterized by the presence of a simple rostral appendage in the form of a modified rostral scale or a complex rostral appendage comprising several scales, sometimes together with postrostrals; the appendage is prominent in males (except in some male specimens of *C. erdeleni*). The genus comprises *Ceratophora aspera* Günther, 1864 [low vegetation dwelling species with horn-shaped cylindrical appendage covered with pointed scales, absent in juveniles and dimorphic in adults], *C. erdeleni* Pethiyagoda & Manamendra-Arachchi, 1998 [subarboreal species with rudimentary or absent appendage], *C. karu* Pethiyagoda & Manamendra, 1998 [ground-dwelling species with rudimentary or absent appendage], *C. stoddartii* Gray, 1835 [subarboreal species with pointed horn-shaped appendage restricted to rostral scale, absent in juveniles and dimorphic in adults], *C. tennentii* Günther, 1861 [arboreal species with a laterally compressed leaf-shaped appendage, elliptical and covered with granular scales present in juveniles and monomorphic in adults], and the recently described *C. ukuwelai* Karunarathna, Poyarkov, Amarasinghe, Surasinghe, Bushuev, Madawala, Gorin & de Silva, 2020 [rare and elusive species found on the forest floor in dense forest patches, bearing a long, complex and rough rostral appendage in males]. In general, horns of male *Ceratophora* are larger than female horns and are movable (Pethiyagoda & Manamendra-Arachchi 1998). It seems that the leaf-shaped appendage of *C. tennentii* plays a role in crypsis whereas sexual selection seems involved in other species of the genus. The appendage is present in juveniles and monomorphic (no sexual dimorphism) in adults of *C. tennentii* (Whiting et al. 2015). In *C. aspera* and *C. stoddartii*, it is horn-shaped, effectively absent in juveniles and dimorphic (sexual dimorphism present) in adults (Johnson et al. 2013). These differences suggest that the appendage evolved independently in *C. tennentii* vs. *C. aspera* and *C. stoddartii*. While the phenotypic similarities between *C. aspera* and *C. stoddartii* might be consistent with homology, such homology is however refuted by the wide separation of these two species in the phylogeny obtained by Johnson et al. (2013). Their combined phenotypic and phylogenetic evidence suggests that rostral appendages evolved independently at least three times in *Ceratophora* (see also Pethiyagoda & Manamendra-Arachchi 1998, Schulte et al. 2002, Karunarathna et al. 2020). Another possible explanation for the existence of such ornaments is that rostral appendages in *Ceratophora* improve crypsis

by breaking up the lizard's outline (Senanayake 1979, Stuart-Fox & Ord 2004). This hypothesis would predict that the appendage should be present in both juvenile and adult lizards, and would not require that it is sexually dimorphic among adults. This may apply to *C. tennentii*, a slow-moving arboreal lizard of the cloud forests (Senanayake 1979, Pethiyagoda & Manamendra-Arachchi 1998). The crypsis hypothesis is unlikely to apply in *C. aspera* and *C. stoddartii* because in these taxa the rostral appendage is sexually dimorphic (Johnson et al. 2013). The absence of a rostral appendage in juveniles and its sexually dimorphic nature in two species of the genus rather suggest that it may function as a sexually selected ornament. However, although the appendage is horn-like in both taxa, there are some important differences concerning allometry relative to sex: a strong positive allometry was identified in males only. This suggests that positive sexual selection may be acting to increase the size of the appendage in male *C. aspera* which have smaller snout–vent lengths than females. Both male and female *C. aspera* are cryptically colored against the leaf litter in the lowland forest where they live (Pethiyagoda & Manamendra-Arachchi 1998). The dimorphic rostral appendage in this species may most likely function in mate or rival recognition (Johnston et al. 2013). While *C. aspera* is widely distributed in the lowland moist forests in Sri Lanka's south-western wet zone, all the other species in the genus are restricted to areas of undisturbed cloud forest between 760 and 2200 m above sea level (Pethiyagoda & Manamendra-Arachchi 1998).

There is one more group of Asian agamids not belonging to the subfamily Draconinae, where particularly the males bear a kind of rostral excrescence, viz. the sailfin agamas of the genus *Hydrosaurus* Kaup, 1828. It is not really an appendage, rather it is a longitudinally directed hump on the snout (Denzer et al. 2020) which shapes, however, the head silhouette of these big-growing lizards and may therefore play a role in the social behavior of these lizards.

Chameleons with rostral appendage

The second group of acrodont iguanians with numerous species adorned with rostral appendages are the chameleons, highly derived, primarily arboreal lizards characterized by bulbous, independently moving eyes, specialized grasping feet, prehensile tails and a unique, body-long protrusible tongue. They are concentrated in the Afro-Malagasy realm with a few species entering the southwestern Palearctic and Oriental regions, and are biologically diverse (Tolley & Herrel 2014). Of the eleven genera currently recognized, one ground-dwelling (*Palleon* Glaw, Hawlitschek & Ruthensteiner, 2013) and two tree-dwelling genera (*Calumma* Gray, 1865 and *Furcifer* Fitzinger, 1843) in Madagascar (Glaw 2015), and likewise one ground-dwelling (*Rhampholeon* Günther, 1874) and two tree-dwelling (*Kinyongia* Tilbury, Tolley & Branch, 2006 and *Trioceros* Swainson, 1839) genera in Africa (Tilbury 2018) contain species with rostral appendages.

In Madagascan tree-dwelling species (*Calumma, Furcifer*) these appendages are either unpaired, compressed ornaments which are partly moveable and soft, partly stiff and supported by a bony rostral process, or forked, likewise bone-supported scaly, diverging processes (Brygoo & Domergue 1968, Brygoo 1971, Glaw & Vences 2007). Also in many of the African tree-dwelling species (*Kinyongia*, *Trioceros*) the males (sometimes also the females) bear rostral appendages. These can be differently shaped single, unpaired scaly projections with or without internal bony support, i.e. flexible or stiff, or they can form a paired bone-supported structure (Tilbury 2018). In several species of *Trioceros*, the head ornamentation consists of annulated horns, most often a single rostral one, supplemented by two preorbital ones. These are supported by bony cones covered by a keratinized, annulated sheath, comparable to the horns of cavicorn (i.e. bovid) mammals. In *Trioceros conirostratus* (Tilbury, 1998), a seemingly rudimentary movable hornlike appendage on the snout tip (Tilbury 2018) strongly resembles that of *Pseudocophotis sumatrana* males (see above). One *Calumma* species group, however, viz. the *C. gallus* group, has a long sword-like rostral appendage (Glaw & Vences 2007, Prötzel 2020) (Fig. 4) resembling in shape that of *Harpesaurus tricinctus* (see Fig. 1) but with a scaled structure like in *Anolis proboscis* (Figs 5, 6c). It is a unique ornamentation among its closer relatives of the *C. nasutum* and *C. boettgeri* groups.

In some African and Madagascan species rostral appendages of males such as bony projections of the snout (e.g. *Calumma brevicorne* (Günther, 1879), or annulated horns typical of the genus *Trioceros* (e.g. *Trioceros jacksoni* (Boulenger, 1896), *T. johnstoni* (Boulenger, 1901), *T. montium* (Buchholz, 1874), *T. oweni* (Gray, 1831)) are used as weapons for intraspecific contests (e.g. Emlen 2008, Stuart-Fox 2014), but they function also for species recognition in sympatric species, as shown already by Rand (1961). He had demonstrated that of the five East African species with three annulated horns none of them is sympatric with a second species bearing the same constellation of horns. According to his table, the same is true for other kinds of rostral appendages. That these head ornaments of the males serve actually as distinguishing cues for mate selection has experimentally been proven by Parcher (1974) who removed the flexible nasal lobe in *C. nasutum* (A. M. C. Duméril & Bibron, 1836) females and thus provoked different reactions of the conspecific males.

Further evidence for the role of head ornamentation in male chameleons as distinguishing optical cues in syntopic species has been provided by Böhme & Klaver (1981). They demonstrated that the natural invasion of a two-horned species (*T. montium*) into the area of the *T. quadricornis* group in West Cameroon lead first to a complete reduction of the horns in *T. q. eisentrauti* (Mertens, 1968), accompanied by an enlargement of the dorsal and caudal sail, plus the replacement of conical gular scales by scaly skin lobes. Subsequently, when *C. montium* conquered also the distribution area of *T. q. quadricornis* (Tornier, 1899), the same morphological change started in the latter: reduced horn size, increased size of the dorsal and tail sails, and accentuation of the gular crest which is weakly developed in *T. montium*. Only the third taxon, *C. q. gracilior* (Böhme & Klaver, 1981), living in the most remote and elevated area of West Cameroon, did not experience penetration of *T. montium* into its range so that it kept its relative longer four horns and lower dorsal and tail sails, thus resembling the silhouette of the allotopic *T. montium* (see the figs. in Böhme & Klaver 1981).
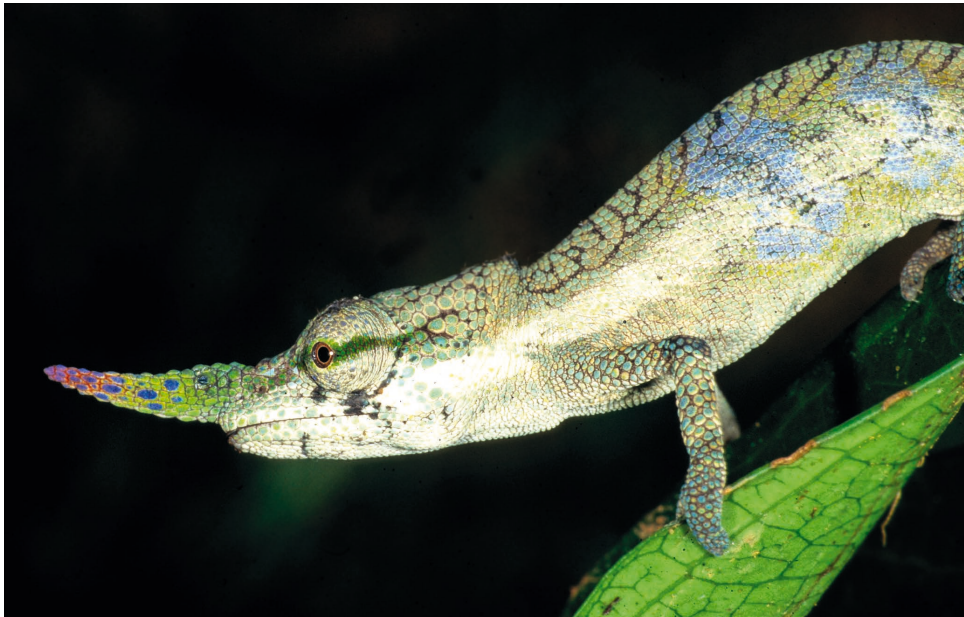

Figure 4. *Calumma gallus* (male) from Madagascar showing its proboscis. Photo: Frank Glaw.

Iguanid lizards with rostral appendage

Horn-like protuberances on the snout occur also in two big-growing iguanids of the genera *Iguana* Laurenti, 1768 and *Cyclura* Harlan, 1824, both named also in respect to these attributes, viz. in *I. iguana rhinolopha* Wiegmann, 1834 of Central America (but see also Breuil et al. 2019) and in *C. cornuta* (Bonnaterre, 1789) occurring on the Caribbean island of Hispaniola. In both cases, the rostral protuberances are comparatively small and seem to serve for mate recognition purposes because *Iguana iguana* (Linnaeus, 1758) shows them only in its *rhinolopha* form which is widely coexisting with the black iguanas of the genus *Ctenosaura* Wiegmann, 1828. Similarly, *Cyclura cornuta* is the only species of this genus with otherwise strictly allopatric insular species which coexists with a sympatric congener on Hispaniola, viz. *C. ricordii* (A. M. C. Duméril & Bibron, 1827). That these large lizards rely on epigamic signals, such as horns, crests, gular sacs etc., in their mating system, is also supported by genital morphological evidence (Ziegler & Böhme 1997). Therefore, the differences in head ornamentation described above are again best explained by character displacement developed in lizards living in syntopy (Breuil et al. 2019).

Dactyloid lizards with rostral appendage

A rostral appendage or proboscis at the front of the snout, like that of *Harpesaurus tricinctus*, is also a distinctive feature of some species of the highly diverse genus *Anolis* Daudin, 1802 (Iguania, Dactyloidae) collectively called proboscis-bearing anoles. Only three species of proboscis-bearing anoles have been so far described: *Anolis laevis* Cope, 1875, *A. phyllorhinus* Myers & Carvalho, 1945, and *A. proboscis* Peters & Orcés, 1956. All are rare arboreal forest lizards with distributions encompassing the Pacific Chocó in Ecuador (*A. proboscis*), Amazonian Peru (*A. laevis*), and Brazilian central Amazonia (*A. phyllorhinus*). They were represented by only nine voucher specimens in 1979 (Williams 1979). In 1956, Peters & Orcés, based on the rarity of all these proboscis-bearing species, known only from males, even suggested that they might correspond to species previously described based on females only. However, there are few species known only from females in that lizard group and that hypothesis is no longer tenable according to recent observations. Among them, *A. proboscis* is particularly convergent with *H. tricinctus* not only by the size and shape of its rostral appendage but also by its habitus and a similar color pattern of broad dorsal alternating dark and light bands (Fig. 5). The convergence for the coloring is particularly pronounced in certain details such as for example the presence in both species of colored ocelli like spot in the hollow of the armpit in both species (Figs 3, 5, 8). Below we compare proboscis-bearing anole species and suggest the use of recent ecological data obtained from this morphologically convergent proboscis-bearing anole lizard to more precisely define the potential habitat in which to search for finding the rare Javan agamid species.

The *Anolis* radiation comprises five main clades that define groups of species often referred to as 'species series' (Castañeda & de Queiroz 2013). Most Amazonian *Anolis* are currently assigned to the *punctatus* group, which includes ca. 20 taxa, some of which exhibit wide ranges in South America. A rostral proboscis can be observed in three species of the genus. Based on the possession of the proboscis, Williams (1979) grouped the three taxa (*A. laevis*, *A. proboscis* and *A. phyllorhinus*) in the *laevis* species group despite they present highly disjunct distribution ranges (see above). Based on morphological characters, *A. proboscis* has been consistently grouped with taxa in the *heteroderma* species group (Poe 2004, Nicholson et al. 2012, Poe et al. 2012, Castañeda & de Queiroz 2013). Morphological comparisons by Yánez-Muñoz et al. (2010) challenged the hypothesis of a close relationship between *A. phyllorhinus* and *A. proboscis*. By contrast,

Figure 5. Among all proboscis bearing lizards, *Anolis proboscis* is the most strongly convergent with the Asiatic agamid *H. tricinctus* and their resemblance is striking. Pichincha: Mindo, Ecuador (QCAZ 10541). Photo: Santiago R. Ron.

other morphological examinations suggested *A. phyllorhinus* as being related to the *punctatus* group (Rodrigues et al. 2002, Yánez-Muñoz et al. 2010). Although genetic data were currently neither available for *A. proboscis* nor for *A. laevis*, recent phylogenetic studies based on combined molecular and morphological evidence suggest that *A. proboscis* is closely related to the *heterodermus* species group (Poe 2004, Nicholson et al. 2012, Poe et al. 2012, Castañeda & de Queiroz 2013). Morphological comparisons, in turn, led Williams (1979) to suggest *A. laevis* to be closely related to *A. heterodermus* A. H. A. Duméril, 1851.

In a recent paper, Prates et al. (2015) infer the relationships of the proboscis-bearing species and demonstrate that *A. phyllorhinus* is the sister taxon of *A. punctatus* Daudin, 1802 in all analyses. The former species is more closely related to the broadly sympatric *A. punctatus* than to the remaining proboscis-bearing species, showing that rostral appendages have evolved independently at least twice in the anole family. Poe et al. (2017) subsequently showed that the three proboscis-bearing anoles belong to three distinct lineages and thus the proboscis has evolved at least three times separately, as it is also the case in the Sri Lankan agamid *Ceratophora* species. Interestingly, with the exception of the proboscis and its reddish dewlap coloration, *A. phyllorhinus* (with proboscis) differs from *A. punctatus* (without proboscis) by only a few quantitative morphological traits. The proper identification of females, which lack both the proboscis and a developed dewlap, is indeed difficult (Rodrigues et al. 2002). Marked structural differences in the probosces of *A. phyllorhinus*, *A. proboscis* and *A. laevis* (see Williams 1979) (Fig. 6 a–c) also support the view that these structures are not homologous (Yánez-Muñoz et al. 2010). *Anolis laevis* has an appendage composed of a single scale (like in *H. tricinctus*; Fig. 7), the rostral plate produced into a flexible appendage (Peters & Orcès 1956) but *A. phyllorhinus* and *A. proboscis* are distinct for they have the snout projection composed of several rows of small scales (see Moraes et al. 2019) (see Figs 6 a,c). The elongated, fleshy appendage of *A. proboscis* differs from that of *A. phyllorhinus* in having a serrated edge and a median dorsal row of scales which is produced into a serrated prominent dorsal crest. The former also possess a very strongly compressed tail with sharp vertebral angle like in *H. tricinctus*.

Among all proboscis-bearing lizards, one anole species, *A. proboscis*, is particularly remarkable since its habitus and color pattern are strongly convergent with its Asiatic agamid counterpart *H. tricinctus*. Below we summarize the ecological data obtained on the three proboscis anoles and particularly the highly convergent *A. proboscis*. Our hypothesis is that similar habitus and coloration of phylogenetically distinct lizards and snakes often reflect a similar ecology and habitat. Thus we suggest using the recent data obtained on the ecology of *A. proboscis* to infer the places where to search for *H. tricinctus* on Java and, as the type locality could not be ascertained because there is no date nor a collector name, also on other Sunda Islands.

Ecology of proboscis-bearing anoles

The Brazilian *Anolis phyllorhinus* was known only from two male specimens until fieldwork in the Amazon a decade ago led to the capture of eight additional specimens, including a female (Rodrigues et al. 2002), and even more specimens recently (Moraes et al. 2019). The moderate-sized proboscis of this anole differs from that of *A. proboscis* since it is shorter and dorsoventrally more enlarged, almost equal to the head size in length; however both are scaly (Fig. 6 a,c). Tail length is much longer than body length and a maximum snout–vent length of 87 mm was noted for a male (Rodrigues et al. 2002).

Observations during that Brazilian expedition provide habitat data for nine specimens, indicating that they occur at varying heights on medium- to large-diameter trees in primary forest; once spotted, most lizards moved higher into the tree. Rodrigues et al. (2002) considered their sample size as too small to indicate microhabitat perch preference. They observed that *A. phyllorhinus* explores virtually all structural habitats on the trunk of thin to thick trees from the ground level to the canopy. Although most of their specimens were first sighted at low heights in trees, they climbed quickly when disturbed, eventually jumping on to branches and leaves. Females have no rostral appendage. Most specimens were brown colored when first sighted. These last specimens were basking at sunny patches on tree trunks, indicating that *A. phyllorhinus*
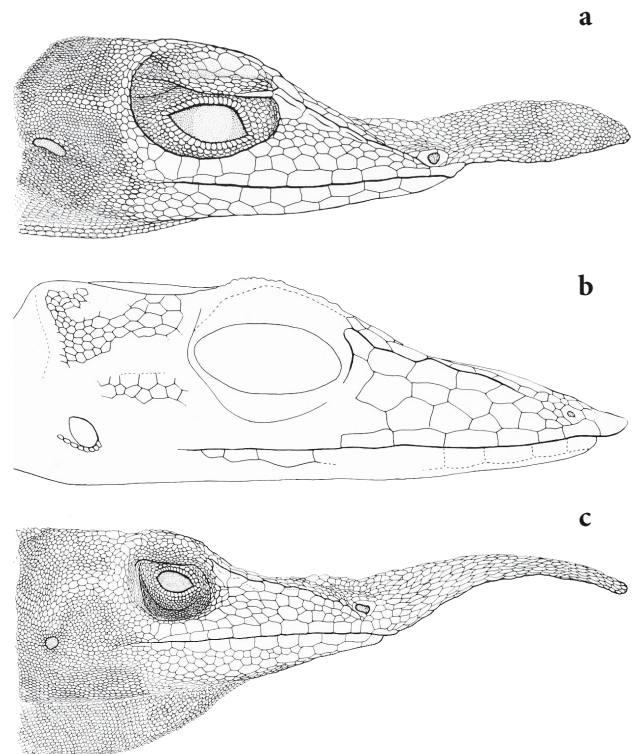
Figure 6. (a) *Anolis phylorrhinus*, (b) *A. laevis*, (c) *A. proboscis*, all after Williams, 1979.

practice behavioral thermoregulation. When spotted, most specimens were in position of territorial survey: pointing downwards, head elevated, and limbs extended. Upon noticing an observer, the green color immediately changed to brown (those already brown clearly even changed to a darker tone), and most tried to escape; climbing the tree, displaying, head bobbing and flashing the bright red dewlap (Rodrigues et al. 2002). That kind of green natural coloration fading to a brownish coloration when threatened was recently described for *Harpesaurus modiglianii* from Sumatra (Putra et al. 2020), and such a behavior can be considered as convergent in several unrelated arboreal lizards. Note that males of *Anolis phyllorhinus* and *A. punctatus* from Aripuanã are also identical in color and size, but have strikingly different dewlaps: very large and creamy-white in *A. punctatus* whereas all males of *A. phyllorhinus* have a small and bright red dewlap (Rodrigues et al. 2002). The female lacks the characteristic male proboscis and, except of a few consistent differences, is morphologically similar to females of *A. punctatus*, a species closely related and broadly sympatric with *A. phyllorhinus*. The most recent data obtained from that species are consistent with the hypotheses that the male proboscis probably evolved as a sexual signal and that visual signals for intra- and interspecific recognition are redundant in anoles (Rodrigues et al. 2002).

Anolis laevis is another distinctive "proboscis anole" known only from the type specimen originating from a mountain trail between Moyobamba and Balsa Puerto in the Department of San Martin, Central Peru (Poe & Yanez-Miranda 2008). It has not been seen from Peru since its description by Cope in 1875 based on a single preserved male specimen (Losos et al. 2012). Its small proboscis (Fig. 6b) is just minimally developed (Williams 1979). The original description by Cope (1875) indicates a total length of 139 mm for a tail of 79 mm.

The third proboscis anole, *Anolis proboscis* (see Fig. 5, 6c), was reported from its type locality in Ecuador at Cununuco (and from Las Tolas, from Lloa-Mindo, and from Tulipe: Yánez-Muñoz et al. 2010). All these localities are on the western slopes of the Andes in Distrito Metropolitano de Quito, province of Pichincha. Poe & Yánez-Miranda (2008) were unable to verify the presence of *A. proboscis* in Peru, and they suspect these are mistaken records. The most likely Ecuadorian endemic *A. proboscis* was an enigma until recently. Known for decades from only six specimens, all being males and last one collected in 1966, nearly four decades passed without a reported sighting until 2005, when ecotourists on a birdwatching trip discovered one lizard crossing a road near the type locality (Almendáriz & Vogt 2007). Subsequently, five more specimens, including the first females, were located in two new areas in 2007 and 2008, extending the species' known distribution 11–13 km northward (Yánez-Muñoz et al. 2010). Eleven more specimens were found near the type locality in 2008 and 2009 (Poe 2010, Losos et al. 2012, Poe et al. 2012).

The snout–vent length of five specimens ranges from 54.4 to 78.1 mm (70.4 ± 9.1 mm). The dorsal crest is covered with 71–92 spiny scales from the neck to above the cloaca (Yánez-Muñoz et al. 2010). Losos et al. (2012) indicated a maximum snout–vent length of 83.6 mm for males and 76.9 mm for females based on examination of 9 males and 11 females. Male has three dorsal lighter bands which do not meet ventrally – one is anterior of front legs, one posterior of front legs and one about midway between front and hind legs (see Fig. 3 in Yánez-Muñoz et al. 2010).

Anolis proboscis is an extremely slow moving species which is cryptic in pattern and coloration. It appears to spend most of its time in dense vegetation high off the ground where it is almost impossible to observe. Indeed, several times when watched with binoculars, lizards were lost due to a slight movement – once as a result of a sneeze, another when the wind blew the vegetation about – and the lizard could not be relocated (Losos et al. 2012). *Anolis proboscis* is clearly a twig anole. In all respects, Losos et al. (2012) considered it as extremely similar to Greater Antillean twig anoles. Morphologically, it has a slender body (as evident by relatively low residual mass), short legs and tail, and a narrow head, all features that characterize twig anoles (Losos 2009) but also their Asian morphological counterpart *H. tricinctus*. Its tail is weakly prehensile, as is that

Figure 7. Holotype of *H. tricinctus* (MNHN-RA 0623) showing the proboscis much longer than head and not covered with scales, having only enlarged scales at its base.

of Greater Antillean twig anoles (e.g., Williams & Rand 1969, Hedges & Thomas 1989). The sexes of *A. proboscis* differ in possession of the horn, and in color and pattern (see Fig. 8; Yánez-Muñoz et al. 2010). One aspect of the crypticity of *A. proboscis* is that it shows rarely display behavior (Losos et al. 2012). This is, however, consistent with a general trend among West Indian anoles, in which twig anoles tend to display less than other ecomorphs. Feeding behavior did not differ markedly between sexes (Losos et al. 2012) although 75% of males, but only 45% of females, had consumed beetles, whereas 25% of males, but 55% of females, had consumed dipterans (see Fig. 9). This also shows that a rostral appendage, only present in males, has no function as a lure to attract insects or other prey. *Anolis proboscis* is a montane species living in a narrow range of altitudinal levels, from 1200 m to about 1400–1600 m with cool dawn air temperatures of 14.5°C (Losos et al. 2012). Yánez-Muñoz et al. (2010) indicate that the species is very difficult to observe in the wild. Four field trips to Las Tolas between July 2007 and September 2008, covering a distance of about 6 km allowed sampling of only four specimens. At Las Tolas, the ratio of *A. proboscis* observations versus other sympatric species (*Anolis aequatorialis* Werner, 1894 and *A. gemmosus* O'Shaughnessy, 1875) was 1:50. They noted that the species' rarity may be due to several factors: (1) naturally low populations; (2) high microhabitat specificity (e.g., canopy); and (3) sampling method effect since the species is cryptic and a typical shrub/arboreal species. According to available data the species was only observed from a small area (33 km²) and lives in a narrow altitudinal range of only 400 m in areas with severe fragmentation and habitat destruction. Most likely it does not prefer to be associated with disturbed habitat but is more visible there compared to deep forest where it certainly occurs preferentially (Ineich 2010). It was most often observed, day and night, on twigs or branches with diameters 1–2 cm, rarely on trunks, whereas it stays on leaves at night, on vines or branches and twigs.

Anolis proboscis often occurs high in the trees. The rostral horn notwithstanding, it is indistinguishable from Greater Antillean anoles of the "twig" ecomorph class in morphology, ecology, and behavior. The possession of a proboscis by males only could suggest a role in sexual selection (Fig. 8). The horn in life is soft and highly flexible (see Fig. 9) and thus unsuitable for use as a weapon in male–male combat; hence, the proboscis most likely serves as an intraspecific communication signal and may be involved in mate choice or territorial displays. Quirola et al. (2017) provided the first data on the role of that appendage in social interactions. By using a semi-natural environment where males and females were placed, they describe social interactions of this species during 11 male–female courtship and mating interactions, as well as three male–male agonistic interactions. They also describe four types of displays by males, many involving the rostral appendage. They found that the rostral appendage is used as an ornament in social displays but not as a weapon in combat. That research reports also the ontogeny of the rostral appendage. Most interesting is the behavior termed "proboscis flourishing": a display composed of stereotyped lateral movements of the head that appear to be a way for the male to present the rostral appendage to the female counterpart. In addition, the paper reports the first captive-born *A. proboscis* among which males are born with a tiny rostral appendage. This study also confirms that the proboscis is actively lifted before any bite attempt and is not, under any circumstance, used as a weapon against other males as previously suggested (Losos et al. 2012, Poe et al. 2012). In

Figure 8. A pair of *Anolis proboscis* in their natural habitat. Photo by Miguel Vences.

contrast, the authors suggest that the movement of the proboscis could be performed to facilitate feeding behaviors or even other behaviors related to courtship as the proboscis was lifted when males stimulate the female's nape (similar to what was described in other anoles). It is now clear that the rostral appendage has no direct use in physical combat. Given its cryptic morphology and behavior, it is not surprising that *A. proboscis* is so rarely observed (Losos et al. 2012).

Suspected ecology of the extinct *Harpesaurus tricinctus*

We now have summarized all available data on proboscis-bearing lizards to try an extrapolation of the ecology of *H. tricinctus* compared to what we know on convergent species. However, sexual dimorphism for horns, if not present in *H. tricinctus*, would be an important evolutionary difference with its convergent dimorphic *Anolis proboscis*. Obviously, *H. tricinctus* can be considered as a typical arboreal canopy dwelling species.

Functional aspects of lizard rostral appendages

Several functional or ecological purposes for the rostral appendage have been suggested (including its use to warm more rapidly in the morning or as a lure to attract prey). It is now demonstrated that the males do not use them as weapons in intrasexual combat. However, the rostral appendage of *A. proboscis* is an extremely flexible structure, bent when it comes into contact, even gently, with other objects (see Fig. 9). It was further suggested that the proboscis simply evolved as a way to make a male look larger (see Fig. 8). Many aspects of the displays of male anoles, and of males of other species of lizard, serve to make individuals look

larger, such as ventrolateral flattening of the body, erection of crests on the neck and back, engorgement of the throat, and extension of the dewlap (Jenssen 1977, Losos 2009). In addition, during aggressive displays to other males, several species of anole will turn sideways, straighten their bodies, and extend their tongues far out of their mouths, perhaps for the same purpose to maximize their apparent body length (Schwenk & Mayer 1991). In general, larger males have a big advantage in male–male combat (reviewed in Losos 2009), so any characteristic that makes one male look larger than another may be useful. Alternatively, females may be more attracted by males with an extended appendage, perhaps because it made those males look larger, or perhaps for other reasons; note that, according to Stuart-Fox & Ord (2004), larger males don't have always advantages. That entire hypothesis could be experimentally tested in captive animals with e.g., robots or artificial proboscis of different lengths and/or colors placed on the snout of males and females.

A number of chameleon species possess soft rostral projections instead of bony horns (e.g., *Calumma* spp., *Rhampholeon* spp., *Kinyongia* spp.), as do a number of agamid lizards in the genera *Lyriocephalus* and *Ceratophora* (Schulte et al. 2002), but the appendages in these lizards are equally poorly understood. In all of these taxa, species exhibit sexual dimorphism in horn size, shape, number, or presence, and some *Ceratophora* have been described moving their horns in a manner similar to that reported by Losos et al. (2012) in *A. proboscis*. The dewlap of *A. proboscis* is not particularly large. This small size may have several explanations. Certainly, the dewlap of *A. proboscis* is smaller than those of the three other sympatric anoles. The small size of the dewlap of *A. proboscis* thus may serve as a species recognition cue, a means for lizards to distinguish conspecifics from sympatric non-conspecifics (Losos & Chu 1998, Nicholson et al. 2007). Alternatively, anoles with smaller dewlaps or no dewlaps at all often have oth-

Figure 9. The flexibility of the rostral appendage of *Anolis proboscis* can be recognized e.g. during food intake (here a male hunting a spider). Photo: Miguel Vences.

er signals, such as colorful body patterns or permanently erect crests (Williams & Rand 1977, Fitch & Henderson 1987, Losos & Chu 1998) or even the ability for vocalization, e.g., *A. vermiculatus* Cocteau, 1837, *A. salvinii* Boulenger, 1885 (its synonym *A. vociferans* pointing on this ability) and others (Milton & Jenssen 1979, Böhme et al. 1985: table).

One final aspect of *A. proboscis*'s snout appendage deserves mention: it is moveable. Observations of Losos et al. (2012) and Poe et al. (2012) concur with those of Quirola et al. (2017), who observed males raising their horns to a 45° angle. Poe et al. (2012) also suggested that males changed the inclination of their horns during social encounters. Anyway the orientation of the appendage changed during the course of behavioral observations. Ecomorphologically, *A. proboscis* and *A. phyllorhinus* are different in many ways (Losos et al. 2012). Compared with *A. proboscis*, *A. phyllorhinus* has longer legs, a longer tail, and is green in color. Ecologically, it does not seem to be a twig specialist. Losos et al. (2012) argued that these ecomorphological differences suggest that possession of a proboscis, whether homologous or convergent, is not associated with a particular ecomorphological lifestyle. However, when associated with other characters like body shape and color pattern, it certainly indicates some similarities in habitat use.

Our examination of proboscis-bearing lizards clearly shows that there is a strong convergence between *Harpesaurus tricinctus* and *Anolis proboscis* concerning habitus and color pattern as well as proboscis size and shape. Both are well in accordance with the Greater Antillean "twig" ecomorph anoles, which are generally cryptically colored, diminutive species with short limbs, narrow heads, and a short, prehensile tail (Losos et al. 2012). However, the later point was not demonstrated for *H. tricinctus*.

One might suspect, in accordance with the observations made on proboscis anoles that females of *H. tricinctus* have been mixed in the past with females of another sympatric species of the genus. This is unlikely since there is no other species of the genus known from Java (if Java is really the origin of that species). Klomp et al. (2016) showed that there is a kind of competition between two principal mechanisms for increasing conspicuousness, either by increasing the ornament's color or brightness contrast against the background and to increase the size of the ornament, which is clearly the case for *H. tricinctus* and *A. proboscis*. Both have a cryptic, banded color pattern and no gular fold or only a weakly developed dewlap. A negative relationship across species between color contrast against the background and dewlap or proboscis size in males, but not in females, suggest that males of different species use increasing color contrast and dewlap/proboscis size as alternative strategies for effective communication and social life. Klomp et al. (2016) also showed that each component in a signal (such as color or size) may be influenced by different selection pressures.

Apart from the different body and tail but similar head shape of the chameleon *Calumma gallus* (Günther, 1877) (Fig. 4), the habitus of *Harpesaurus tricinctus* is strongly convergent with that of the canopy-dwelling *Anolis proboscis*. The presence of a proboscis in anoles is sexually dimorphic and most likely excludes a role in thermoregulation or as a lure to attract prey. Its role could be to increase the observed size of males vis à vis females and/or other conspecific males and also to function as an intraspecific signal. Potential absence of sexual dimorphism of the rostral appendage in *H. tricinctus*, would be an important difference with *A. proboscis*. All possibilities exist among Asian arboreal proboscis-bearing agamid lizards.

Conclusion

We here suggest that *H. tricinctus* should be searched on Java in deep montane moist forest (above 1000 m elevation), most likely on tree trunks and branches around the canopy but also at night when sleeping on low elevation branches. Anyway, as Java cannot be ascertained because there is no collector nor collect locality attached to the holotype specimen, searching on other Sunda Islands also seems realistic to us. Temperature can be cool at dawn and below 14°C. As such lizards may be impossible to be observed in deep forest, we suggest to prospect in freshly deforested timber and agricultural areas where they will be easier to spot at remaining recently created forest edges easy to access (see Ineich 2010). The species certainly will allow reduced time for basking and thus will be difficult to observe. It will capture its prey by a sit and wait strategy, and together with its cryptic coloration, few movements will make eye sightings delicate. According to its banded color pattern, the species certainly will use mosses and lichens in the montane cloud forest for insolation in cold weather condition as well as in higher temperature. Its habitat should present a high vegetative cover with abundant shade, moving sun patches and low amount of bare soil.

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