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Cover image<br>Life photo of adult female of Pachydactylus melachlani Bauer, Lamb, \& Branch, sp. nov. (Reptilia: Gekkota: Gekkonidae) from Farm Sperlingsputs, Karasburg District, Namibia. Photo courtesy of W.H. Haacke.<br>For further details, see Bauer, et. al., this issue, pp. 595-709 (esp. pp. 670 ff ).

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# PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES <br> Fourth Series 

# The Symplocaceae of Gaoligong Shan 

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#### Abstract

A taxonomic revision of the flowering plant family Symplocaceae in the Gaoligong Shan region of western Yunnan Province in China and eastern Kachin State in north－ ern Myanmar is presented．Sixteen species are recognized from the region．The treat－ ment includes a key to species，descriptions，specimen citations，and images of sever－ al species．Also included are species distribution maps based on estimates of geo－ graphic coordinates of old specimens and GPS－derived coordinates of more recent collections．


Keywords：Burma，China，Gaoligong Shan，Kachin，Myanmar， Taxonomy，Symplocaceae，Symplocos，Yunnan


#### Abstract

高黎贡山山砍科 本文对高黎贡山地区的有花植物类群山矾科进行了系统修订，高黎贡山位于中国云南西部，缅甸北方克钦邦东部。研究确认该地区有 16 种本科植物。这一修订包括了分种检索表，文献引证，种的特征描述和根据目前可得到的全部新老标本资料估算得出的地理信息所绘制的种分布图。


关键词：缅甸，中国，高黎贡山，克钦邦，分类订正，山矾科，山矾属，云南

The Gaoligong Shan（GLGS）is a 600 km －long high－elevation mountain range that over much of its length straddles the border between western Yunnan Province in southwestern China and east－ ern Kachin State in northern Myanmar（Burma；Figure 1）．The mountain range extends north in China into the Xizang（Tibetan）Autonomous Region where it runs into the heavily dissected part of the southeastern part of the Qinghai－Xizang Plateau．This north－to－south－oriented range lies between two of Asia＇s great river systems，the Irrawaddy（Ayerawaddy）and the Salween（Nujiang）． Together with the adjacent Himalaya and Hengduan mountain systems，the Gaoligong Shan forms a vast biodiversity hotspot，i．e．，an ecoregion of tremendous biodiversity under severe threat of destruction through human activity（Li et al．2000；Liu and Kress 2005；Stotz et al．2003；Chaplin 2006）．

As part of a long－term，large－scale multidisciplinary biotic survey and inventory of the Gaoligong Shan，we have begun to examine the taxonomy of vascular plant groups of this region in which we have expertise．One such group，Symplocaceae，appeared to us to be in need of taxo－ nomic clarification because of the apparent inconsistency in which Gaoligong Shan specimens have been identified．Here we provide a detailed taxonomic treatment of Symplocaceae for Gaoligong Shan，in the hope that it can serve as a model for similar treatments of other vascular plant groups of interest to us in the region．

The Symplocaceae（Angiospermae：Ericales sensu APG 2003）comprise a single genus of about 325 species of trees and shrubs distributed widely in the tropical and subtropical regions of
the Americas and eastern Asia to Australia. Phylogenetic analysis of Ericales DNA sequences with 11 gene regions supports a clade comprising Styracaceae and Diapensiaceae as the sister group of Symplocaceae (Schönenberger et al. 2005). The monophyly of Symplocos is well established on the basis of morphology and molecular data (Wang et al. 2004; Fritsch et al. 2006; Fritsch and Almeda, in press).

The species of Symplocos in China have been treated taxonomically in various ways. Brand's (1901) work is the last worldwide revision of the genus, but it is now largely outdated. Nooteboom has conducted a comprehensive taxonomic revision of Symplocos of the Old World in several publications (Nooteboom 1975, 1977, 1980, 2005). In the most recent of these, Nooteboom recognized 41 species in China. In the Flora Reipublicae Popularis Sinicae (FRPS), Wu (1987) recognized many more Chinese species (77) of Symplocos. Later, however, Wu modified species concepts in Symplocos to agree more closely with those of Nooteboom, as reflected in the collaborative treatment of Symplocos for Flora of China (Wu and Nooteboom 1996), such that 42 species were recognized in this treatment. Subsequent authors have nonetheless maintained recognition of some FRPS segregate Symplocos species (e.g., Chen et al. 2003; Ye et al. 2003).

The only comprehensive work to address the flora of Myanmar is a checklist of the country's seed plants (Kress et al. 2003) as revised from earlier editions by other authors. In this work, 37 species of Symplocos are listed for Myanmar, but it is clear that many of these are best treated as synonyms of other species, and the 17 species of Symplocos reported from Myanmar by Nooteboom (2005) should be taken as the more accurate estimate.

Flora of Gaoligong Mountain (Li et al. 2000) comprises a list of all vascular plant species in the Gaoligong Shan known up to the time of its publication. For each species, it provides information on distribution (in descriptive form), habit, habitat, elevation, and locality, and cites representative voucher specimens for each species. Although our list of species largely agrees with that of Li et al. (2000), it differs in several notable respects. Li et al. recognize 15 species and four varieties of Symplocos from the region, with one species endemic, whereas we recognize 16 species and no varieties, and none of the species are endemic to the region. Five species in our treatment are new to the region (i.e., they are not listed in Li et al., either as a species recognized by us or as a synonym), and four additional names are new (i.e., four species in Li et al. are synonyms of species that are not listed by them). We could not locate the cited voucher specimens of two Symplocos species included in Li et al. (2000), viz., those of S. groffii Merrill (X.C. Shi \& S.X. Yang 537 and Gaoligong Shan Vegetation Expedition 2-116) and S. hookeri C.B. Clarke (X.C. Shi 353); therefore we could not confirm the membership of these species in the Gaoligong Shan flora. Other differences between our treatment and that of Li et al. (2000) are discussed under relevant species entries.

## Materials and Methods

More than 1000 collections from nine herbaria were studied. The material examined comprises the Gaoligong Shan collections from PE and KUN, the two herbaria with the richest collections in SW China, and also those from A, BM, CAS, E, K, P, and W. Only collections that occur within the GLGS region (Figure 2) as defined by Chaplin (2006) were included. Figure 3 gives the political units at the level of county or district in the GLGS region. Many of the collections have resulted from a biotic survey and inventory project primarily involving staff from KUN, CAS, and E, at which the first, second, and third sets from most of these expeditions, respectively, have been deposited. At the time this Symplocos treatment was completed there had been 11 collecting expeditions undertaken in the context of this inventory, all of which use the same series of collecting numbers; these are referred to herein as "GLGS" collections. The various teams collecting under


FIGrefe 1 Satellite image covering the GLGS region and adjacent part of China and Myanmar. Modified from red line) and adjacent part of China and Myanmar showing Cloudless Mosaic N-47-20_loc and N-47-25_loc 1989-1994 range in meters: < 305, 305-914, 914-2134 2134-3353. > obtained from the Global Land Cover Facility, University of 3353.
this number series that appear on specimen labels are listed in Appendix 1, as are abbreviations for other major collectors or collecting teams (with ten or more Symplocos collections) that have conducted expeditions to Gaoligong Shan.

Species descriptions are derived from examination of herbarium specimens except where noted. Most of the species have been seen in the field by the authors, and characters such as flower color have been confirmed. Descriptions generally reflect character variation occurring only within the Gaoligong Shan region. Flowering and fruiting times, elevation ranges, habitats, distributions, common names, and uses were derived from label information of herbarium specimens. Specimen information of all collections examined was entered into a database. For specimens without geographic coordinates indicating collecting locality, coordinates were estimated whenever possible by using the descriptive information on the label and georeferencing with published maps and gazetteers. The database was then linked to the geographic information system software ArcView (ESRI, Inc.), with which all distribution maps were constructed. The coordinates for specimens with locality information considered too vague were not mapped.

The vast majority of expeditions has taken place within the Chinese part of the Gaoligong Shan region. The paucity of species distribution points in Myanmar, therefore, in many or most cases is likely to result from the absence of data rather than the absence of the species from the area. If a major survey and inventory operation in the Myanmar portion of the range were to be initiated, we expect that more species of Symplocos from the flora region would be documented. The Northern Triangle area between the N'mai Kha and Mali Kha rivers has been surveyed relatively well by F. Kingdon Ward and others, and we have seen two species from this region (Symplocos dolichotricha Merrill and S. macrophylla Pancher ex Guillaumin) that can be expected to occur in the Myanmar portion of the Gaoligong Shan as well.

The collections of George Forrest have proven difficult to map because often only a latitude and elevation are specified on labels, in which case it is not certain on which side of the range the specimen was collected. (There is a strong probability that any particular specimen was collected on the west side, closest to Tengchong, because that city was Forrest's base of operations, but this is not discernable in any specific case.) Further, the coordinates and elevation sometimes do not agree with the description of the general area in which the collection was made. In his later years, Forrest depended heavily on native collectors to reach areas of difficult access (both for physiographic and political reasons). The label information of many of Forrest's collections is based on his interpretations of these collectors' notes. Thus it is difficult to map Forrest's collection local-
ities with any degree of precision. We have nonetheless mapped many of them because of their historical importance, although they are presented with the caveat that they should be considered general and interpreted with caution. The database of collections examined with estimates of geographic coordinates is available from the authors and at the web site www.calacademy.org.

Synonymy generally includes only names based on material from Gaoligong Shan or other provinces in southwestern China or northern Myanmar. Other synonyms are provided when nomenclaturally or taxonomically significant, as needed. When numerous synonyms exist, as in the case of, e.g., widespread or complex taxa, only names based on types from Gaoligong Shan or adjacent areas are included, other than the accepted name when its type does not come from Gaoligong Shan. In these cases, reference to works with a more detailed or complete synonymy is provided.

Botanical terminology generally follows that of Harris and Harris (2001).

## Taxonomic Treatment of Symplocaceae

Symplocos Jacquin, Enum. Syst. Pl., a 5, b 24. 1760.
TyPE: Symplocos martinicensis Jacquin.
Bobua Adanson, Fam. Pl. 2:88, 526. 1763 ('Bobu’). Type: Bobua laurina (Retzius) de Candolle (lectotype, designated by Nooteboom 1975) [ $\equiv$ Symplocos laurina (Retzius) Wallich ex G. Don].
Hopea Linnaeus, Mant. Pl. 1:105. 1767 and Syst. Nat., ed. 12, 2:509. 1767, nom. rej., non Roxburgh (1811). Protohopea Miers, J. Linn. Soc., Bot. 17:289. 1879. Type: Hopea tinctoria Linnaeus (lectotype, designated by Nooteboom 1975) [ $\equiv$ Symplocos tinctoria (Linnaeus) L'Héritier].
Drupatris Loureiro, Fl. Cochinch. 1:314. 1790. Type: Drupastris cochinchinensis Loureiro (lectotype, designated by Nooteboom 1975) [= Symplocos cochinchinensis (Loureiro) S. Moore].
Decadia Loureiro, Fl. Cochinch. 1:315. 1790. Type: Decadia aluminosa Loureiro (lectotype, designated by Nooteboom 1975) [= Symplocos laurina Wallich ex G. Don].
Dicalix Loureiro, Fl. Cochinch. 2:663. 1790. Type: Dicalix cochinchinensis Loureiro (lectotype, designated by Nooteboom 1975) [ $\equiv$ Symplocos cochinchinensis (Loureiro) S. Moore].
Lodhra Guillemin, Ann. Sci. Nat., Bot. 15:158. 1841, nom. illeg.; (G. Don) Decaisne in Jacquemont, Voy. Inde. 4:104. 1844, quoad basionym, excl. species. Basionym: Symplocos section Lodhra G. Don, Gen. Hist. 4:2. 1837. Type: Symplocos racemosa Roxburgh (lectotype, designated by Nooteboom 1975) [ Symplocos racemosa Roxburgh].
Palura (G. Don) Miers, J. Linn. Soc., Bot. 17:297. 1879. Basionym: Symplocos (subgen. Symplocos) section Palura G. Don, Gen. Hist. 4:3. 1837. Type: Symplocos crataegoides Buchanan-Hamilton ex D. Don (lectotype, designated by Nooteboom 1975) [= Symplocos paniculata (Thunberg) Miquel].
Cordyloblaste Henschel ex Moritzi, Bot. Zeitung (Berlin) 6:606. 1848. Type: Cordyloblaste henschelii Moritzi (lectotype, designated by Nooteboom 1975) [ $\equiv$ Symplocos henschelii (Moritzi) Bentham ex C.B. Clarke].

Shrubs or trees, evergreen or rarely deciduous. Stipules absent. Leaves spirally (GLGS) or distichously arranged, simple, margin of young leaf blade glandular, glands caducous or persistent. Inflorescences spikes, racemes, panicles, or glomerules, rarely 1-flowered. Pedicel usually subtended by 1 bract. Flowers actinomorphic, bisexual (GLGS) or rarely unisexual, fragrant, typically subtended by 2 bracteoles. Hypanthium completely adnate to ovary. Calyx limb (3-)5-lobed (5-lobed in GLGS), persistent. Corolla gamopetalous ca. half total length (rare in GLGS) or only at base. Margin of corolla lobes distinct except at base; lobes (3-)5(-11) (5 in GLGS), imbricate. Stamens usually numerous, adnate only at base of corolla or rarely (GLGS) ca. half their length, monadelphous or loosely pentadelphous; filaments terete or tangentially flattened; anthers subglobose, 2-locular. Ovary inferior, unilocular, incompletely 2-5-septate; ovules 2-4 per locule. Epigynic disk or ring present, persistent. Style 1, filiform; stigma capitate or prominently 2-5-lobed. Fruit a drupe; endocarp (1-)3(-5)-locular. Seeds with copious endosperm; embryo straight or curved; cotyledons
much shorter (GLGS) or somewhat longer than radicle.
One genus and ca. 325 species (Fritsch and Almeda, in press): widely distributed in tropics and subtropics of Asia, Australia, and America; 41 species (18 endemic) in China (Wu and Nooteboom 1996; Nooteboom 2005); ca. 17 species in Myanmar (Kress et al. 2003; Nooteboom 1975, 2005), none endemic; 16 species in Gaoligong Shan, none endemic.

## Key to Species of Symplocos in Gaoligong Shan

* indicates species with two entries in key

1a. Articulation immediately below hypanthium absent; corolla gamopetalous and stamens adnate to corolla ca. half the total length; corolla lobes papillose adaxially; filaments abruptly constricted apically, papillose; fruit fusiform
9. S. pendula

1b. Articulation immediately below hypanthium present; corolla gamopetalous and stamens adnate to corolla only at base; corolla lobes smooth adaxially; filaments not abruptly constricted apically, smooth; fruit not fusiform.
2a. Deciduous; inflorescences pseudo-terminal (but bracts sometimes leaf-like)
8. S. paniculata

2b. Evergreen; inflorescences pseudo-terminal and axillary.
3a. Leaf blade midvein adaxially prominent at least toward base.
4a. Pseudo-terminal buds strigillose or lanate-sericeous; young branchlets densely appressed-hirtellous, trichomes incurved; mature branchlets grayish; pedicel present ( $2-5 \mathrm{~mm}$ ); hypanthium strigillose; fruit strigillose
.1. S. anomala
4b. Pseudo-terminal buds glabrous (margins often ciliolate); young branchlets glabrous or rarely sparsely tomentellous, puberulent, or lanate, trichomes not incurved; mature branchlets greenish, often purplish mottled; pedicel absent; hypanthium glabrous; fruit glabrous
.14. S. theifolia
3b. Leaf blade midvein adaxially impressed.
5a. Hypanthium and fruit pubescent.
6a. Young branchlets lanate to tomentose; leaf blade abaxially lanate; inflorescence rachis, bracts, bracteoles, hypanthium, calyx lobes, and fruit pilose or sericeous
12. S. sulcata

6b. Young branchlets strigose, hispidulous, puberulent, or glabrous; leaf blade abaxially strigose or glabrous; inflorescence rachis, bracts, bracteoles, hypanthium, calyx lobes, and fruit strigose, strigillose, puberulent, or glabrous.

7a. Petiole $5-12 \mathrm{~mm}$; leaf blade abaxially typically drying green or pale brown, adaxially often minutely hispidulous on midvein or occasionally glabrous, secondary veins $6-10$ on each side of midvein, apex longacuminate; fruit ellipsoid
11. S. ramosissima*

7 b. Petiole $2-6 \mathrm{~mm}$; leaf blade abaxially typically drying pale green or pale grayish green, adaxially glabrous, secondary veins $3-5(-7)$ on each side of midvein, apex caudate; fruit narrowly ampulliform, or rarely subglobose at maturity. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 15. S. viridissima
5b. Hypanthium and fruit glabrous.
8a. Inflorescences glomerulate, rachis not evident.
9a. Petiole $18-35 \mathrm{~mm}$; leaf blade $17-25 \mathrm{~cm}$, abaxially glaucous, papillose toward base; longest stamens $3-4 \mathrm{~mm}$; fruit ovoid-ampulliform, $12-18 \times$ 6-8 mm; endocarp smooth
4. S. glauca

9b. Petiole 6-12 mm; leaf blade $8-18 \mathrm{~cm}$, abaxially not glaucous, not papillose; longest stamens $7-9 \mathrm{~mm}$; fruit cylindrical or ellipsoid-cylindrical, $6-9 \times 2.5-3.5 \mathrm{~mm}$; endocarp ribbed . . . . . . . . . . . . . . . . 5. S. glomerata 8 b. Inflorescences with rachis evident.

10a. Disk pubescent.
11a. Bracts deltoid; bracteoles deltoid; inflorescence rachis white-strigillose.
7. S. oxyphylla

11b. Bracts broadly ovate to suborbicular; bracteoles broadly ovate, suborbicular, linear, lanceolate, or oblanceolate; inflorescence rachis tawny-, yellow-, or ferrugineous-lanate-villous to -pilose.
12a. Pseudo-terminal vegetative buds $9-16 \mathrm{~mm}$, outer scales glabrous or strigillose; leaf blade apex acuminate; bracteoles linear, lanceolate, or oblanceolate; calyx lobes $0.5-1 \times 0.6-0.8 \mathrm{~mm}$; disk inconspicuous . . . . . . . . . . . . . . . . . . . . . . 3. S. dryophila
12b. Pseudo-terminal vegetative buds $2-6(-8) \mathrm{mm}$, outer scales sericeous or lanate; leaf blade apex acute to obtuse; bracteoles broadly ovate to suborbicular; calyx lobes $1.3-1.8 \times 1.2-1.8 \mathrm{~mm}$; disk annual-pentagonal to 5 -lobed
10. S. racemosa

10b. Disk glabrous.
13a. Bracts persistent; bracteoles covering most or all of hypanthium; fruit $4.5-7 \mathrm{~mm}$.

14a. Young branchlets tomentose; mature branchlets brown to black; inflorescences $5-10.5 \mathrm{~cm}$, rachis tomentose; calyx lobes

14b. Young branchlets glabrous or strigose; mature branchlets greenish; inflorescences $0.4-5.9 \mathrm{~cm}$, rachis strigillose or pilulose; calyx lobes glabrous; style $1-3 \mathrm{~mm}$ 6. S. laurina

13b. Bracts caducous (rarely persistent or semi-persistent in S. ramosissima and S. sumuntia); bracteoles covering less than half of hypanthium; fruit (6-)7-29 mm.
15 a. Vegetative buds $2.5-4 \mathrm{~mm}$; leaves typically drying yellowish green, apex abruptly acuminate to caudate; inflorescences villous; fruit ampulliform to ovoid
13. S. sumuntia

15 b. Vegetative buds $4-11 \mathrm{~mm}$; leaves typically drying green to brown, apex acuminate or long-acuminate; inflorescences puberulent or glabrous; fruit ellipsoid to obovoid.

16a. Vegetative buds $4-8 \mathrm{~mm}$, pubescent at least along distal portion of outer scale midvein; leaf blade secondary veins 6-10 on each side of midvein, margin crenulate-serrulate; bracteoles usually persistent; fruit $7-11 \times 4-6 \mathrm{~mm}$; endocarp indurate throughout. . . . . . . . . . . . . . . 11. S. ramosissima* 16b. Vegetative buds $8-13 \mathrm{~mm}$, glabrous except for ciliolate scale margins; leaf blade secondary veins 13-17 on each side of midvein, margin entire; bracteoles caducous; fruit $24-29 \times$ ca. 12 mm ; endocarp with indurate part irregularly intercalated with network of softer spongy tissue
16. S. xylopyrena

1. Symplocos anomala Brand, Bot. Jahrb. Syst. 29:529. 1900. Bobua anomala (Brand) Migo, Bot. Mag. (Tokyo) 56:267. 1942. Dicalix anomalus (Brand) Migo, Bull. Shanghai Sci. Inst. 13:198. 1943. Type.- China. Sichuan: northern Wushan, A. Henry 7094 (lectotype [designated by Nooteboom 1975]: E; isolectotype: K!).

Symplocos alata Brand, Bot. Jahrb. Syst. 29:529. 1900.
Symplocos argentea Brand, Pflanzenr. 6(IV. 242):67. 1901.
Symplocos dielsii H. Léveillé, Repert. Spec. Nov. Regni Veg. 9:445. 1911.
Symplocos esquirolii H. Léveillé, Repert. Spec. Nov. Regni Veg. 9:445. 1911.
Symplocos fusonii Merrill, Philipp. J. Sci. 15:251. 1919. S. anomala Brand var. fusonii (Merrill) Handel-
Mazzetti \& E. Peter, Beih. Bot. Centralbl. 62(B):24. 1943. Dicalix fusonii (Merrill) Migo, Bull. Shanghai Sci. Inst. 13:201. 1943.
Symplocos anomala Brand var. liosiphon Handel-Mazzetti, Symb. Sinicae 7:808. 1936.
Symplocos anomala Brand var. nitida H.L. Li, J. Arnold Arbor. 24:452. 1943.
Shrubs or trees, evergreen, to 5 m tall. Young branchlets densely white- to brown-appressedhirtellous, trichomes at least slightly incurved; mature branchlets grayish; pseudo-terminal vegetative buds 3-9 mm, strigillose to lanate-sericeous. Petiole 3-7 mm, usually sparsely and minutely glandular, glands frequently caducous; leaf blade typically oblong-elliptic to oblong-oblanceolate, less commonly narrowly elliptic, elliptic, or oblanceolate, 4.5-11.5 $\times 1.6-3.9 \mathrm{~cm}, 2.5-3.8$ times as long as wide, subcoriaceous, typically drying abaxially green, yellowish green, or grayish green and adaxially yellowish green to dark green, abaxially glabrous or occasionally strigose along midvein, adaxially glabrous or occasionally uncinate-hirtellous on midvein, midvein adaxially prominent, secondary veins $7-18$ on each side of midvein, base attenuatecuneate, margin entire or finely serrulate and revolute, apex acuminate. Inflorescences pseudo-terminal and axillary raceme-like cymes, $0.7-1.4 \mathrm{~cm}, 1-8$-flowered; rachis white-, yellow-, or yellowish fer-rugineous-strigillose; bract apex acute. Bracts and bracteoles ovate to deltoid, nearly isomorphic but bracts slightly larger, $0.4-1.3 \times 0.3-1.3$ mm , persistent, strigillose, margin ciliolate and often glandular. Pedicel $2-5 \mathrm{~mm}$; bracteoles covering less than half of hypanthium, apex rounded, obtuse, or acute. Hypanthium white- or brown-strigillose, subtending articulation present. Calyx limb gamosepalous for $0-0.6 \mathrm{~mm}$; lobes semi-oblong, semi-elliptic, or semi-orbicular, $0.5-1.5 \times 0.9-1.5 \mathrm{~mm}$, strigillose or occasionally glabrous, margin ciliolate and often glandular, apex obtuse to occasionally acute. Corolla white or pale green, $4-5 \mathrm{~mm}$, membranous, gamopetalous only at base; lobes narrowly elliptic, glabrous, adaxially smooth. Stamens ca. 30-60, adnate to corolla only at base, longest 5-6 mm; filaments not abruptly constricted apically, smooth. Disk pentagonal and 5-lobed, hirtellous. Style 4-7 mm, glabrous. Fruit brown, globose to cylindrical, $5-12 \times 4-6 \mathrm{~mm}$, strigillose; endocarp indurate throughout, 3 locules developed, perimeter faintly ribbed. Seeds straight.

This species is easily distinguished from other species of Symplocos in Gaoligong Shan by the combination of its adaxially prominent leaf blade midvein and pubescent pseudo-terminal buds. It is widespread throughout southern China but has only been rarely collected in Gaoligong Shan.

Selected Illustrations.- R.F. Wu, Flora Reipublicae


Figure 4. Distribution map of Symplocos anomala in the GLGS region.

Popularis Sinicae 60（2）：18 t．4（12－15）．1987；G．H．Zhu，ed．Fl．China Ill．15：t．173（12－15）． 2000.
Phenology．－Fl．and fr．Apr－Dec．
Distribution and habitat．－Mixed forests；1600－2000 m．In GLGS：CHINA．Yunnan： Fugong Xian（Shangpa Zheng），Longling Xian（The eighth district），Tengchong Xian（Puchuan Xiang）；Figure 4．Outside of GLGS：Anhui，Fujian，Guangdong，Guangxi，Guizhou，Hainan，Hubei， Hunan，Jiangsu，Sichuan，Taiwan，Xizang，Yunnan，Zhejiang［Indonesia，Japan（Okinawa）， Malaysia，Myanmar，Thailand，Vietnam］．

Local name．－薄叶山矾 bao ye shan fan
Additional specimens examined．－CHINA．YUNNAN：FUGONG XIAN．Shangpa Zheng． The valley behind the first middle School，W of Fugong，1600－1700 m， 30 Sep 1997，GLGS 9778 （E，KUN）； $2700 \mathrm{~m}, 10$ Oct 1933，Tsai 54376 （A）； $2700 \mathrm{~m}, 19$ Oct 1933，Tsai 54459 （A，KUN）； $2000 \mathrm{~m}, 20$ Sep 1933，Tsai 56561 （A，KUN）．LONGLING XIAN．Tian Ling Temple， $2400 \mathrm{~m}, 10$ Aug 1941，Wang 90011 （KUN）；Hong Mu Shu， 15 Aug 1941，Wang 90066 （KUN）；Hong Mu Shu， 2400 m ，Wang 90118 （KUN）；the eighth district， 18 Aug 1941，Wang 90160 （KUN）．TENGCHONG XIAN．Puchuan Xiang．The ninth district，1880－1980 m， 8 Oct 1960，W．C．Yin 60－1383（KUN）．

2．Symplocos cochinchinensis（Loureiro）S．Moore，J．Bot．52：148．1914．Basionym：Dicalix cochinchinensis Loureiro，Fl．Cochinch．2：663．1790．Dicalix cochinchinensis Loureiro，Fl． Cochinch．2：663．1790．Type．－Vietnam：＂Cochinchina，＂J．de Loureiro s．n．（lectotype［designat－ ed by Nooteboom 1975］：BM）．

Drupatris cochinchinensis Loureiro，Fl．Cochinch．1：314． 1790.
Symplocos cochinchinensis var．puberula M．S．Huang \＆Y．F．Wu，Acta Phytotax．Sin．24：202． 1986.
Trees，evergreen，to 9 m tall．Young branchlets brown－tomentose；mature branchlets dark brown to black；pseudo－terminal vegetative buds $5-7 \mathrm{~mm}$ ，brown－tomentose．Petiole $0.9-1.7 \mathrm{~cm}$ ， not glandular；leaf blade elliptic， $18-22.5 \times 7-10.1 \mathrm{~cm}, 2-3.3$ times as long as wide，subcoriaceous， typically drying yellowish green to green，abaxially yellow－，ferrugineous－，or brown－villous，－ tomentose，or－pilose，densely so on principal veins，adaxially brown－to ferrugineous－tomentose proximally on midvein，otherwise glabrous，midvein adaxially impressed，secondary veins 8－12 on each side of midvein，base broadly cuneate，margin serrulate，revolute，apex acute，acuminate，or occasionally emarginate through tip abortion．Inflorescences pseudo－terminal and axillary simple or more often branched spike－like cymes， $5-10.5 \mathrm{~cm}, 10-\mathrm{ca}$ ． 40 －flowered；rachis densely reddish brown－to yellowish brown－tomentose．Bracts and bracteoles broadly ovate to orbicular，isomorphic but bracts usually larger， $1.5-4 \times 1.8-3.5 \mathrm{~mm}$ ，persistent，densely strigillose，margin ciliate，not glandular，apex acute to rounded．Pedicel absent；bracteoles keeled，covering most or all of hypan－ thium．Hypanthium glabrous，subtending articulation present．Calyx limb not gamosepalous；lobes suborbicular，1．3－2 $\times 1.3-1.7 \mathrm{~mm}$ ，sericeous，margin ciliate，not glandular，apex obtuse to rounded． Corolla white，3－5 mm，membranous，gamopetalous only at base；lobes narrowly oblong，glabrous， adaxially smooth．Stamens ca． $50-70$ ，adnate to corolla only at base，longest $4-6 \mathrm{~mm}$ ；filaments not abruptly constricted apically，smooth．Disk annular，glabrous．Style $3.5-5 \mathrm{~mm}$ ，glabrous．Fruit ampulliform to globose， $4-7 \times 4-5 \mathrm{~mm}$ ；glabrous；endocarp indurate throughout， 1 locule devel－ oped，perimeter finely ribbed．Seeds twice－curved．

Symplocos laurina is often treated within the circumscription of S．cochinchinensis，but here we treat the two as distinct species．See discussion under S．laurina．Only the Gongshan Xian spec－ imen can be mapped with confidence；the Fugong Xian specimen does not indicate a more precise locality and may be on the non－Gaoligong Shan side of the Nujiang．

Selected Illustrations．－Y．F．Wu，Fl．Reipubl．Popularis Sin．60（2）：59 t．21（8－10）．1987；

G．H．Zhu，ed．Fl．China Ill．15：t．189（11－13）． 2000.
Phenology．－Fl．Aug－Sep，fr．Oct－Nov．
Distribution and habitat．－Mixed forests； $1100-2200 \mathrm{~m}$ ．In GLGS：CHINA．Yunnan：Fugong Xian（Shangpa Zheng），Gongshan Xian（Dulongjiang Xiang）；Figure 5．Outside of GLGS：S Fujian， Guangdong，Guangxi，Hainan，Jiangxi，Sichuan，Taiwan，Xizang， Yunnan，Zhejiang［India，Indonesia，Japan，Laos，Malaysia， Myanmar，Papua New Guinea，Philippines，Thailand，Vietnam］．

Local name．－越南山胡 yue nan shan fan
Uses．－Timber used for making furniture．Seeds oil used in industry．

Additional specimens examined．－CHINA．Yunnan： FUGONG XIAN．Shangpa Zheng． 2000 m， 1 Oct 1934，Tsai 59127 （A， KUN）．GONGSHAN XIAN．Dulongjiang Xiang．From Bapo to Maku， $1500 \mathrm{~m}, 15$ Aug 1982，QX 9358 （KUN）．

3．Symplocos dryophila C．B．Clarke in J．D．Hooker，Fl．Brit． Ind．3：578．1882．Type．－IndiA．Sikkim：8000－10000 ft．，J．D． Hooker s．n．（Herb．Ind．Or．J．D．Hooker \＆T．Thomson 53）（holotype： K！；isotypes：BM！，GH！，L，P，W！）．

Symplocos delavayi Brand，Repert．Spec．Nov．Regni Veg．3：218． 1906. Dicalix delavayi（Brand）Migo，Bull．Shanghai Sci．Inst．13：200． 1943.
Symplocos longipetiolata Rehder in Sargent，Pl．Wilson．2：599． 1916.
Symplocos forrestii W．W．Smith，Notes Roy．Bot．Gard．Edinburgh 13：185．
1921．Dicalix forrestii（W．W．Smith）Migo，Bull．Shanghai Sci．Inst． 13：201． 1943.
Dicalix shunningensis Migo，Bull．Shanghai Sci．Inst．13：205． 1943.


Figure 5．Distribution map of Symplocos cochinchinensis in the GLGS region．

Shrubs or trees，evergreen，to 10 m tall．Young branchlets glabrous or more often proximally white－to tawny－sericeous to－pilose；mature branchlets purplish；pseudo－terminal vegetative buds $0.9-1.6 \mathrm{~cm}$ ，outer scales glabrous or strigillose，inner scales usually strigose to sericeous．Petiole $0.8-1.9 \mathrm{~cm}$ ，not glandular；leaf blade elliptic，oblong－elliptic，obovate，or oblanceolate， $7.4-14.5 \times$ $1.9-5.0 \mathrm{~cm}, 2.3-4.8$ times as long as wide，subcoriaceous，typically drying abaxially pale green to yellowish green and adaxially green to yellowish green，abaxially glabrous or rarely sparsely pilose along midvein，adaxially glabrous，midvein adaxially impressed，secondary veins 5－17 on each side of midvein，base cuneate，margin serrulate or occasionally entire and planar or rarely slightly rev－ olute，apex acuminate．Floral buds axillary，globose，4－10 mm；scales suborbicular to orbicular， glabrous or strigillose．Inflorescences pseudo－terminal and axillary，simple or rarely branched racemes or spikes， $1.6-7.5 \mathrm{~cm}, 12-22$－flowered，frequently shorter and with fewer flowers distally； rachis tawny－，yellow－，or pale ferrugineous－lanate to－pilose；bract broadly ovate to suborbicular， $5-6 \times 3-5 \mathrm{~mm}$ ，apex obtuse to rounded．Bracts and bracteoles caducous，densely sericeous，not glandular．Pedicel 0－2 mm；bracteoles linear，lanceolate，or oblanceolate， $1-6 \times 0.1-1.2 \mathrm{~mm}$ ，cov－ ering less than half of hypanthium．Hypanthium glabrous，subtending articulation present．Calyx limb gamosepalous for 0 to ca． 0.3 mm ；lobes deltoid， $0.5-1 \times 0.6-0.8 \mathrm{~mm}$ ，glabrous or rarely sparsely sericeous，margin entire or ciliate and not glandular，apex acute with a blunt tip．Corolla white or yellow，4－5 mm．membranous．gamopetalous only at base；lobes $\pm$ oblong－elliptic， glabrous，adaxially smooth．Stamens ca．45－60，adnate to corolla only at base，longest $5-7 \mathrm{~mm}$ ；fil－ aments not abruptly constricted apically，smooth．Disk inconspicuous，annular or 5－lobed，strig－
illose to pilulose. Style 3.5-5 mm, glabrous. Fruit blue, ellipsoid-cylindrical, 5-10 $\times 3-4.5 \mathrm{~mm}$, glabrous: endocarp indurate throughout, 2 or 3 locules developed, perimeter smooth. Seeds straight.

This is one of the most common species of Symplocos in the Gaoligong Shan, and is often observed in abundance as a subdominant understory tree. In the sterile condition it is easily distinguished from other species of Symplocos by its conspicuous ( $4-10 \mathrm{~mm}$ ) globose axillary floral buds.

Selected Illustrations.- R.F. Wu, Fl. Reipubl. Popularis Sin. 60(2):44 t. 16(1-4). 1987; G.H. Zhu, ed. Fl. China Ill. 15:t. 186(1-4). 2000.

Photographic images.- Figures 6-7.
Phenology. - Fl. Mar-Jun, fr. Jul-Nov.
Distribution and habitat.- Mixed evergreen and deciduous broadleaf forest, Coniferous


Figure 6. Flowering branch of Symplocos dryophila. Photo by M. Dickson.
forest，Deciduous broadleaf forest，Subtropical evergreen broadleaf forest，Thicket；1300－3500 m． In GLGS：CHINA．Xizang：Zayü Xian（Tsarong Xiang）．Yunnan：Fugong Xian（Lishadi Xiang， Lumadeng Xiang，Shangpa Zheng），Gongshan Xian（Bingzhongluo Xiang，Cikai Zheng， Dulongjiang Xiang），Longling Xian（Longjiang Xiang），Lushui Xian（Chen＇gan Xiang，Liuku Zheng，Luzhang Xiang，Pianma Xiang），Tengchong Xian（Guyong Zheng，Qushi Xiang，Wuhe Xiang，Zhonghe Xiang），MYANMAR．KACHIN：Myitkyina District（Chibyaw Township）；Figure 8．Outside of GLGS：Guangdong，Guangxi，Hainan，SW Sichuan，Yunnan［India，Myanmar， Thailand，Vietnam］．

## Local name．—坚本山矾 jian mu shan fan．

Additional specimens examined．－CHINA．XIZANG：ZAYÜ XIAN．Chaw－ji Pass， 9000－10000 ft．， 20 May 1920，R．J．Farrer 1564 （E）； $2800 \mathrm{~m}, 18$ Jul 1973，QX 73－774（KUN）．Tsarong Xiang． SE Xizang， $9000-10000 \mathrm{ft}$ ．，May 1922，F 21620 （A，E，K）；Mount Kenyichunpo and region of Champutong， Salween－Irrawaddy watershed，1923，Rock 10246 （A，W）；N slopes of Mt．Kenichunpo，N of Sikitung，upper Salween River， 11000 ft．， 1 May 1932，Rock 22116 （A，E，K）；N slopes of Mt．Kenichunpo，N of Sikitung， upper Salween River， 10000 ft ．，May－Jun 1932，Rock 22118 （A，E，K）．YUNNAN：W Slope of Gaoligong Shan，1540－3500 m， 15 Jul 1979，Bijiang Expedition 972 （KUN［2］）；1917－1919，F 16067 （K）；1917－1919， F 17805 （A，K）；1917，F 26635 （K）；F 29837 （E）；bank of Kiukiang，NW of Sbchin， 1700 m， 25 Jul 1937，Yü 19400 （KUN［2］）．FUGONG XIAN． 2700 m， 21 Jun 1978，Bijiang Expedition 609 （KUN［2］）；Shala Valley， 2900 m， 16 Jul 1978，Bijiang Expedition 1187 （KUN）；DaZhi team to Mashiding， 2350 m， 1 Aug 1979，Bijiang Expedition 1945 （KUN［2］）．Lishadi Xiang．Moist canyon just S of the Shibali Logging Station on the rd from the Nujiang to Yaping Pass，E side of Gaoligong Shan， 2506 m， 28 Apr 2004，GLGS 19993 （CAS）；between Shibali Logging Station and Yaping Pass，ca． 4 km W of Shibali，from the Nujiang to Yaping Pass，E side of Gaoligong Shan， 2785 m， 2 May 2004，GLGS 20090 （CAS）；between Shibali Logging Station and Yaping


Figlre 7．Fruiting branch of Symplocos dryophila．Photo by Lihua Zhou．

Pass, ca. 4.1 km W of Shibali, from the Nujiang to Yaping Pass, E side of Gaoligong Shan, 3007 m, 2 May 2004, GLGS 20150 (CAS); between the Nujiang and Shibali Logging Station, ca. 16 km W of the Nujiang, from the Nujiang to Yaping Pass, E side of Gaoligong Shan, 2181 m, 7 May 2004, GLGS 20383 (CAS); Yaduo Cun, above Shibali, on S side of the N fork of Yamu He, along the rd to the Myanmar border at Yaping Yakou, E side of Gaoligong Shan, 2830 m, 6 Aug 2005, GLGS 26543 (CAS); Yaduo Cun, above Shibali on the way to the Myanmar border at Yaping Yakou, N side of the N fork of Yamu He, E side of Gaoligong Shan, $2750 \mathrm{~m}, 10$ Aug 2005, GLGS 26909 (CAS); loc. cit., GLGS 26910 (CAS); loc. cit., GLGS 26913 (CAS); loc. cit., GLGS 26918 (CAS); Yaduo Cun, above Shibali along the N side of S fork of Yamu He, E side of Gaoligong Shan, $2800 \mathrm{~m}, 15$ Aug 2005, GLGS 28359; Yaduo Cun, Luodigoulu, N side of N fork of Yamu He, E side of Gaoligong Shan, $2520 \mathrm{~m}, 16$ Aug 2005, GLGS 28431 (CAS); loc. cit., GLGS 28432 (CAS). Lumadeng Xiang. Rd along the S fork of the Yamu River, on the rd to Amero Pass, ca. 23 km SW of the confluence of the N and S forks of the Yamu, E side of Gaoligong Shan, 3022 m, 2 May 2004, GLGS 20292 (CAS); Yaping Cun, below Amero Pass along the rd back down to the confluence of the N and S fork of Yamu He, E side of Gaoligong Shan, 3120 m, 13 Aug 2005, GLGS 27168 (CAS); Yaping Cun, vicinity of Mapa, below Amero Pass, along a ridge from the rd using the old trail down to the S fork of Yamu He, E side of Gaoligong Shan, 3100 m, 13 Aug 2005, GLGS 27228 (CAS); Yaping Cun, above the southern Shibali, along the S fork of Yamu He, on the rd to Amero Pass, E side of Gaoligong Shan, $2800 \mathrm{~m}, 14$ Aug 2005, GLGS 27278 (CAS); loc. cit., GLGS 27280 (CAS); Yaping Cun, Shibali, on the S side of N fork of Yamu He, E side of Gaoligong Shan, $2510 \mathrm{~m}, 16$ Aug 2005, GLGS 28470 (CAS); loc. cit., GLGS 28486 (CAS); loc. cit., GLGS 28487 (CAS); 2900 m, 28 May 1982, QX 7018 (KUN [2]). Shangpa Zheng. 20 Oct 1933, Tsai 54487 (A). GONGSHAN XIAN. Bingzhongluo Xiang.


Figure 8. Distribution map of Symplocos dryophila in the GLGS region. 2400 m, 25 Jun 1982, QX 7692 (KUN [2]); Xiaohe, bank of Nujiang, 13 Nov 1959, Wu 24558 (PE); 13 Nov 1959, Feng 24567 (KUN [3]); 13 Nov 1959, Feng 54558 (KUN [3]); Gongdan Holy Hills, E side of Gaoligong Shan, along the trail from Bingzhongluo to top of Holy Hills, 2500 m, 17 Apr 2002, GLGS 14444 (CAS); Gongdan Holy Hills, E side of Gaoligong Shan, along the trail from Bingzhongluo to top of Holy Hills, 2500 m, 17 Apr 2002, GLGS 14461 (CAS, KUN); Gongdan Holy Hills, E side of Gaoligong Shan, along the trail from Bingzhongluo to top of Holy Hills, 2000 m, 17 Apr 2002, GLGS 14473 (CAS, KUN); loc. cit., GLGS 14474 (CAS, KUN); Gongdan Holy Hills, E side of Gaoligong Shan, along the trail from Bingzhongluo to top of Holy Hills, 2540 m, 24 Apr 2002, GLGS 14669 (CAS, KUN); loc. cit., GLGS 14689 (CAS, KUN); Gong Dang (God's Mountain) beyond the end of the rd to a marble quarry just SW of Bingzhongluo, E side of Gaoligong Shan, $2620 \mathrm{~m}, 9$ Oct 2002, GLGS 17103 (CAS, KUN); $2650 \mathrm{~m}, 24$ Jun 1982, QX 7456 (KUN [2]). Cikai Zheng. 5 km from Qiqi towards Dongshaofang, $2400 \mathrm{~m}, 21$ Sep 1997, GLGS 9509 (E, KUN); E side of divide above Dong Shao Fang forest station on Nan Mo Wang Shang, $3400 \mathrm{~m}, 22$ Sep 1997, GLGS 9531 (E, KUN [2]); E side of Gaoligong Shan, along the Danzhu He on the rd from Nu Jiang at Danzhu to the Myanmar border, $2750 \mathrm{~m}, 1$ Jul 2000, GLGS 11843 (CAS, GH, KUN); E side of Gaoligong Shan, W of Gongshan, along a branch of the Pula He, W of Rizhidi Bridge on the trail from Qiqi to Dongshao Fang and the Dulong Jiang Valley, 2100-2200 m, 11 Jul 2000, GLGS 12300 (CAS, GH, KUN); E side of Gaoligong Shan, below Xiaoxue Cao along the Danzhu He on the rd from the Nu Jiang at Danzhu to the Myanmar border, 2610 m, 2 Jul 2000, GLGS 12307 (CAS, GH, KUN); E side of Gaoligong Shan, W of Gongshan, Qiqi above the Pula He, 2300-2570 m, 12 Jul 2000, GLGS 12507 (CAS, GH, KUN); Heiwadi, E side of Gaoligong Shan, along the Pula He on the new rd to Dulong Jiang Valley, $2210 \mathrm{~m}, 12$ Apr 2002, GLGS 14135 (CAS, KUN); E side of Gaoligong Shan, W of Gongshan, along the Pula He on the trail from Qiqi to No. 12 Bridge and Dulongjiang Valley, $2500 \mathrm{~m}, 3$ May 2002, GLGS 14874 (CAS, KUN); along rd from Gongshan to Kongdang, E side of Gaoligong Shan, $2750 \mathrm{~m}, 23$ Sep 2002, GLGS 16521 (CAS, KUN); E side
of Gaoligong Shan on the rd from Gongshan to Kongdang, 2720 m, 12 Nov 2004, GLGS 23052 (CAS). Dulongjiang Xiang. W bank of Nujiang, Sicui, Maku, 2000 m, 17 Nov 1959, Feng 24336 (KUN [3]); Bapodi, 2000 m, 10 Nov 1959, Feng 24425 (KUN [4]); Sandui, NE of Shigong Bridge and NW of Xishaofang on the trail from Gongshan to Bapo, 22 Nov 1990, GLGS 742 (CAS, KUN [3]); Sandui, NE of Shigong Bridge, 1900 m, 22 Nov 1991, GLGS 785 (KUN [2]); Maku, southern region of the Dulong Jiang Valley on the W side of the Dulong Jiang, $1950 \mathrm{~m}, 16$ Dec 1990, GLGS 1095 (CAS, KUN); Maku, southern region of the Dulong Jiang Valley on the W side of the Dulong Jiang, $2020 \mathrm{~m}, 16$ Dec 1990, GLGS 1107 (CAS, KUN); along the Mabiluo River which is the most northeastern tributary of the Dulong Jiang, $1310 \mathrm{~m}, 30$ Dec 1990, GLGS 1393 (CAS, KUN [2]); Meiliwang, along the trail from Bapo to Gongshan on the E side of the Dulong Jiang, $1900 \mathrm{~m}, 14$ Jan 1991, GLGS 1943 (KUN); Meiliwang, 2300 m, 16 Jan 1991, GLGS 3056 (KUN [2]); Meiliwang, along the trail from Bapo to Gongshan on the E side of the Dulong Jiang, 2100 m, 16 Jan 1991, GLGS 3066 (CAS, KUN [2]); along the Dandangwang He, NW of Bapo on the W side of the Dulong Jiang, $1400 \mathrm{~m}, 16$ Jan 1991, GLGS 3145 (CAS, KUN [2]); along the Dandangwang He, NW of Bapo on the W side of the Dulong Jiang, 1350 m , 16 Jan 1991, GLGS 3167 (KUN [2]); Maku, southern region of the Dulong Jiang Valley on the W side of the Dulong Jiang, $2000 \mathrm{~m}, 8$ Mar 1991, GLGS 4290 (CAS, KUN [2]); Maku, southern region of the Dulong Jiang Valley on the W side of the Dulong Jiang, $2000 \mathrm{~m}, 13$ Mar 1991, GLGS 4579 (CAS, KUN [2]); loc. cit., GLGS 4584 (CAS, KUN [2]); Maku, 2100 m, 13 Mar 1991, GLGS 4600 (KUN [2]); Qiawudang, S side of the Gamolai He, ca. 4 km SE of Bapo on the E side the Dulong Jiang, $2100 \mathrm{~m}, 22$ Mar 1991, GLGS 4779 (CAS, KUN); Qiawudang, Dulongjiang, 2100 m, 22 Mar 1991, GLGS 4780 (KUN [3]); Qiawudang, Dulongjiang, 2100 m, 22 Mar 1991, GLGS 4781 (KUN [2]); Qiawudang, Kaladi, 2350 m, 23 Mar 1991, GLGS 4865 (KUN [2]); Shigong Bridge, between Xishaofang and Bapo on the trail from Gongshan to Bapo, $2200 \mathrm{~m}, 24$ Mar 1991, GLGS 4941 (KUN [2]); Qiawudang, S side of the Gamolai He, ca. 4 km SE of Bapo on the E side the Dulong Jiang, $2500 \mathrm{~m}, 25$ Mar 1991, GLGS 4968 (CAS, KUN [2]); along the Wangmei He, N of the trail from Bapo to Gongshan and NW of Xishaofang on the E side of the Dulong Jiang, $2200 \mathrm{~m}, 26$ Mar 1991, GLGS 5203 (KUN [2]); along the Wangmei He, N of the trail from Bapo to Gongshan and NW of Xishaofang on the E side of the Dulong Jiang, $2100 \mathrm{~m}, 26$ Mar 1991, GLGS 5204 (KUN [2]); Langbendang, middle region of the Dulong Jiiang on the W side, $2100 \mathrm{~m}, 26$ Mar 1991, GLGS 5229 (KUN [2]); Langbendang, middle region of the Dulong Jiiang on the W side, $2150 \mathrm{~m}, 27$ Mar 1991, GLGS 5236 (CAS, KUN [2]); Xishaofang, 3200 m , 20 Mar 1991, GLGS 5257 (KUN); Xishaofang, along the trail from Gongshan to Bapo on the E side of the Dulong Jiang, $3200 \mathrm{~m}, 30$ Mar 1991, GLGS 5357 (CAS, KUN); Longyuan, ca. 6 km S of Dizhengdang on the W side of the Dulong Jiang, 1650 m, 11 Apr 1991, GLGS 5405 (KUN [2]); Longyuan, ca. 6 km S of Dizhengdang on the W side of the Dulong Jiang, $1650 \mathrm{~m}, 11$ Apr 1991, GLGS 5467 (KUN [2]); Longyuan, ca. 6 km S of Dizhengdang on the W side of the Dulong Jiang, $1700 \mathrm{~m}, 11$ Apr 1991, GLGS 5500 (KUN); Dizhengdang, 1880 m , 13 Apr 1991, GLGS 5703 (KUN [2]); Xuebalaka. ca. 7 km SE of Dizhengdang between Kongdang and Dizhengdang on the E side of the Dulong Jiang, 2100 m, 15 Apr 1991, GLGS 5919 (CAS, KUN); Wangnulaka, ca. 5 km NW Dizhengdang, on the W side of the Dulong Jiang, $2500 \mathrm{~m}, 18$ Apr 1991, GLGS 6074 (KUN); Chi Ba Ji, $2400 \mathrm{~m}, 17$ Apr 1991, GLGS 6111 (KUN [2]); Silaolaka, ca. 5 km SW Dizhengdang, on W side of the Dulong Jiang, $2400 \mathrm{~m}, 21$ Apr 1991, GLGS 6293 (CAS, KUN); $2500 \mathrm{~m}, 16$ May 1991, GLGS 6840 (KUN [2]): 2500 m. 22 May 1991, GLGS 7024 (KUN [2]); Sandui, NE of Shigong Bridge and NW of Xishaofang on the trail from Gongshan to Bapo, 2700 m, 22 May 1991, GLGS 7038 (KUN [2]); S of the second team. Dulongjiang. 22 May 1991, GLGS 7049 (KUN [2]): W side of Gaoligong Shan, W of Gongshan, below the pass on the trail from Qiqi to Bapo in the Dulong Jiang Valley, $2800 \mathrm{~m}, 18$ Jul 2000, GLGS 12949 (CAS, KUN): Xianjiudang. W side of Gaoligong Shan, along Dulongjiang Valley on the trail from Kongdang to Dizhengdang. 1560 m, 23 Jul 2002. GLGS 15208 (CAS, KUN); vicinity of Sandui campsite between Shigong Qiao and Xixiaofang on trail from Bapo to Gongshan via Qiqi on the W side of Gaoligong Shan, $2500 \mathrm{~m}, 29$ Oct 2004, GLGS 21981 (CAS): Zhizizhu, $2700 \mathrm{~m}, 9$ May 1979, Nujiang Expedition 71 (KUN [2]): Qiqi. $2200 \mathrm{~m}, 18$ Jul 1982, QX 8093 (KUN [2]); Qiqi, $2000 \mathrm{~m}, 19$ Jul 1982, QX 8207 (KUN [2]): Qiqi. 2000 m .19 Jul 1982. QX 8267 (KUN [2]): Jidu to Dongshaofang, $2600 \mathrm{~m}, 22$ Jul 1982, QX 8426 (KUN [2]): Maku, $2200 \mathrm{~m}, 6$ Aug 1982. QX 8920 (KUN [3]): Maku. $1900 \mathrm{~m}, 6$ Aug 1982, QX 8935 (KUN): Kongdang to Xianjiudang. 1600 m .23 Sep 1982, QX 9553 (KUN); Xianjiudang, $1700 \mathrm{~m}, 24$ Aug 1982. QX 9607 (KUN): Longyuan River, 1900 m .29 Aug 1982. QX 9744 (KUN); Longyuan, $2300 \mathrm{~m}, 30$ Aug 1982. QX 9785 (KUN): Bapo, E bank of Dulong River. 10 Nov 1959. Wu 24125 (PE); Kiukiang Valley, Taron,

2000 m, 19 Aug 1938, Yü 19904 (A, KUN); Taron-Taru Divide, Tangtehwang, 1850 m, 27 Aug 1938, Yü 19994 (A). LONGLING XIAN. Daba, $2400 \mathrm{~m}, 18$ Aug 1941, Wang 90165 (KUN). Longjiang Xiang. Xiaoheishan, 2800 m .26 Jul 1982, QX 8644 (KUN [2]); $2800 \mathrm{~m}, 26$ Jul 1982, QX 8777 (KUN [2]); Xiaoheishan, 2000 m , 28 Jul 1959, Wang 89818 (KUN). LUSHUI XIAN. Tiemu Xiang, 2700 m, 21 Jun 1978, Bijiang Expedition 1761 (KUN [2]); Shanghong, Caijaba, 2900 m, 14 Mar 1989, H. Sun et al. 1655 (KUN); Shanghong, Caijaba, $2100 \mathrm{~m}, 25$ Mar 1989, H. Sun et al. 1656 (KUN); 2800 m , 25 Jan 1942, Wang 89739 (KUN). Chen'gan Xiang. N'Maikha-Salween divide, Close to upper Burma, Aug 1925, F 27211 (A, E, K). Liuku Zheng. ShweliSalween divide, N of Ho-tou, 7000-8000 ft., May 1925, F 26335 (A, E, W); Shweli-Salween divide, 9000 ft ., May 1925, F 26377 (A, E, K). Luzhang Xiang. Yaojiaping, $2200 \mathrm{~m}, 14$ Mar 1989, GLGS 89 (KUN); rd from Pian Ma to Liuku, between Pian Ma Ya Kou and Yao Jia Ping Forest Station, E slope of Salween/Irrawaddy Divide, 2750-2850 m, 5 Oct 1997, GLGS 10059 (E); just below the Fengxue Yakou (the pass between Lushui and Pianma), between km 54 and 58, E side of Gaoligong Shan, $3125 \mathrm{~m}, 19$ May 2005, GLGS 24535 (CAS). Pianma Xiang. Fengxue Yakou, 2800 m, 27 Jul 1978, Bijiang Expedition 1350 (KUN [2]); vicinity of Km 62 on the rd from Lushui to Pianma, W side of Gaoligong Shan, 2790 m, 17 May 2005, GLGS 23307 (CAS); vicinity of Feng Xue Yakou (Windy and Snowy Pass) on rd from Lushui to Pianma, W side of Gaoligong Shan, 3127 m, 11 May 2005, GLGS 23935 (CAS); Wuzhong Village, 2400 m, 4 Aug 1964, Wu 8006 (KUN [2]); Zhong Pianma, 2800 m, 13 Jul 1964, Wu 8020 (KUN [2]); 13 Jul 1964, Wu 8125 (KUN [2]); Wuzhong Village, 2800 m , 25 Jul 1964, Wu 8217 (KUN [2]); Pianma Yakou, 2200 m , 14 Aug 1964, Wu 8363 (KUN). TENGCHONG XIAN. 7000-8000 ft., 1 Sep 1925; Shweli River drainage basin to summit of Shweli-Salween watershed E of Tengyueh, 9000 ft ., Nov 1922, Rock 7669 (A). Guyong Zheng. Hills NW of Tengyueh, 8000 ft ., $F$ 11909 (A, E, K, W); hills around Tengyueh, F 27202 (A, E, K, W); Houqiao, 2950 m, 20 May 1964, Wu 6752 (KUN); Houqiao, 2950 m, 20 May 1964, Wu 6762 (KUN); Houqiao, 3200 m, 1 Jun 1964, Wu 6893 (KUN); Liangyashan, 3000 m, 8 Jun 1964, Wu 7098 (KUN [2]); Liangyashan, 7 Apr 1980, D.Y. Xia 7 (KUN); Liangyashan, 14 Apr 1980, D.Y. Xia 74 (KUN [2]); Changping Batou to Liangyashan, Danzha, 2940 m, 15 Apr 1980, L.S. Xie 877 (KUN [2]). Jietou Xiang. W flank of the Shweli-Salween divide, $8000-9000 \mathrm{ft}$., 1914, F 8991 (BM, K); Shweli-Salween divide, 8000, F 12093 (E); Shweli-Salween divide, 10000 ft., Jul 1917, F 15653 (E [2], K); Shweli-Salween divide, 9000-10000 ft., F 15654 (A, E, K); loc. cit., F 15668 (A, E); loc. cit., F 16007 (A, E, K); Shweli-Salween divide, 8000-9000 ft., Jul 1917, F 15771 (A, E, K); loc. cit., F 18311 (E, K); Shweli-Salween divide, Jul 1918, F 17627 (A, E, K, W). Qushi Xiang. Daba, Gaojiaoyan (High Foot Rock), $2780 \mathrm{~m}, 16$ May 1997, Z.L. Dao et al 9465 (KUN [2]); Shweli-Salween divide, 10000 ft ., Jul 1917, F 15814 (A, K, W); Jul 1918, Shweli-Salween divide, 9000 ft., F 17717 (E, K); Shweli-Salween divide, 6000-7000 ft., F 17780 (A, E, K, W); 1917-1919, Shweli-Salween divide, 7000 ft., Apr 1924, F 24018 (E, K); Liangyashan to Diantan, 2800 m, 10 Jun 1964, Wu 7123 (KUN). Ruidian Xiang. Shweli Valley, 6000 ft., F 12056 (A, E, K). Tengyue. Divide between the Shweli and Tengyueh valleys, $6000-7000 \mathrm{ft}$., Jun 1912, F 8241 (E, K). Wuhe Xiang. Km 24.7 along hwy S 317, Xiaodifang Village and vicinity, W side of Gaoligong Shan, 2169 m, 25 May 2005, GLGS 24882. Zhonghe Xiang. Lava bed W of Tengyueh, 5000 ft., Jun 1912, F 8147 (E). MYANMAR. Upper Burma, 1914, F. Kingdon Ward 16 (E [3]). KACHIN: Shing Hong Pass, N Burma, 10000 ft ., 18 Jun 1920, R.J. Farrer 1621 (E). MIYTKYINA DISTRICT. Laikam-Fengshui, 8000 ft ., 22 Apr 1938, W.D. Kermode 17208 (K); W of Hpawte, 10000 ft., 2 May 1938, W.D. Kermode 17282 (K); Laluga and Htebu, 7000-9000 ft., 13 May 1953, Tha Hla 3955 (K). Chibyaw Township. Tawgaw, NE frontier, 1 May 1912, I.A. Abbay 16 (E); hills around Tzi-tzo-ti, 9000 ft., May 1925, F 26467 (A, E, K); hills around Tzi-tzo-ti, 9000 ft ., Oct 1925, F 27411 (A, E, K); above Langyaw, 6000-7000 ft., 30 Mar 1938, W.D. Kermode 16694 (K) ; between Sadon and the Yunnan-Chinese border at Changtifang and Kambaiti, 1 Nov 1922, Rock 7402 (A).
4. Symplocos glauca (Thunberg) Koidzumi, Bot. Mag. (Tokyo) 39:313. 1925. Basionym: Laurus glauca Thunberg in Murray, Syst. Veg., ed. 14, 383. 1784. Litsea glauca (Thunberg) Siebold, Verh. Batav. Genootsch. Kunsten 12:24. 1830. Myrsine thunbergii Tanaka, Bull. Sci. Fak. Terk. Kjusu Imp. Univ. 1:201. 1925. Bobua glauca (Thunberg) Nakai, Trees Shrubs Japan, Revis. Ed. 1:322. 1927. Dicalix glauca (Thunberg) Migo ex H. Hara, Enum. Spermatophytarum Japon. 1:104. 1948. TYPE.- JAPAN. C.P. Thunberg s.n. (holotype: UPS).

Symplocos grandis Handel－Mazzetti，Beih．Bot．Centralbl．62（B）：15． 1943.
Symplocos oblanceolata Y．F．Wu，Acta Phytotax．Sin． 24 （3）：198． 1986.
Trees，evergreen，to 8 m tall．Young branchlets ferrugineous－to brown－lanate；mature branch－ lets dark brown；pseudo－terminal vegetative buds $6-10 \mathrm{~mm}$ ，ferrugineous－to brown－lanate．Petiole $1.8-3.5 \mathrm{~cm}$ ，not glandular；leaf blade elliptic，oblanceolate，or obovate， $17-25 \times 3-9 \mathrm{~cm}, 2.8-4.5$ times as long as wide，subcoriaceous，typically drying abaxially pale greenish white to greenish brown and glaucous and drying adaxially green to brown，abaxially glabrous or black to brown lanate and minutely papillose at least proximally，adaxially glabrous or occasionally white－or fer－ rugineous－lanate especially along midvein，midvein adaxially impressed，secondary veins 7－16 on each side of midvein，base cuneate，margin entire，denticulate，or serrulate and revolute，apex acuminate，abruptly acuminate，acute，or occasionally obtuse and often rounded or emarginate through tip abortion．Inflorescences pseudo－terminal or axillary，simple or basally branched glomerules，often produced in axils of leaf scars on proximal leafless regions of branchlets， $0.8-1.5$ cm ，to 20 －flowered；rachis not evident；bract orbicular，margin erose and often glandular．Bracts and bracteoles $1.8-3 \times 0.8-3 \mathrm{~mm}$ with bracts larger than bracteoles，persistent，ferrugineous－to dark brown－tomentose，apex rounded．Pedicel absent；bracteoles broadly spatulate，margin entire and not glandular，covering less than half of hypanthium．Hypanthium glabrous，subtending articulation present．Calyx limb gamosepalous for $0.5-1 \mathrm{~mm}$ ；lobes semi－oblong， $0.8-1.3 \times 0.5-1.3 \mathrm{~mm}$ ，fer－ rugineous－to dark brown－tomentose，margin entire or tomentose and not glandular，apex rounded． Corolla white or yellow， $3-5 \mathrm{~mm}$ ，membranous，gamopetalous only at base；lobes narrowly oblong， glabrous，adaxially smooth．Stamens ca．15－30，adnate to corolla only at base，longest 3－4 mm；filaments not abruptly constricted apically， smooth．Disk annular to cylindrical，glabrous or villous．Style 2．5－5 mm ，glabrous．Fruit bluish black，ovoid－ampulliform， $1.2-1.8 \times$ $0.6-0.8 \mathrm{~cm}$ ，glabrous；endocarp indurate throughout， 1 locule devel－ oped，perimeter smooth．Seeds straight．

Selected Illustrations．－R．F．Wu，Fl．Reipubl．Popularis Sin．60（2）：31 t．10（8－10）．1987；G．H．Zhu，ed．Fl．China Ill．15：t． 180（8－10）． 2000.

Phenology．－Fl．Apr－Aug，fr．Aug－Oct．
Distribution and habitat．－Thicket， $2400-2500 \mathrm{~m}$ ．In GLGS：China．Yunnan：Tengchong Xian（Jietou Xiang）；Figure 9. Outside of GLGS：Fujian，Guangdong，Guangxi，Hainan，Hunan， Sichuan，Taiwan，Yunnan，Zhejiang［India，Japan，Myanmar， Thailand，Vietnam］．

LOCAL NAME．－羊舌树 yang she shu
Uses．－Bark used medicinally．
ADditional specimens examined．－CHINA．YUNNAN： 8000 ft．，Jun 1924，F 24641 （K）．TENGCHONG XIAN．Jietou Xiang．Shweli－ Salween divide， 9000 ft ．，Nov 1924，F 25241 （E．K）．

This species has apparently not been collected since Forrest＇s expedition in 1924．The locality information of only one of the Forrest collections is specific enough by which to estimate geograph－ ic coordinates．

5．Symplocos glomerata King ex C．B．Clarke in J．D．Hooker，Fl． Brit．Ind．3：577．1882．Dicalix glomeratus（King ex C．B．Clarke）


Figure 9．Distribution map of Symplocos glauca in the GLGS region．

Migo, Bull. Shanghai Sci. Inst. 13:201. 1943. Type.- IndiA. Assam (Khasia Hills) or Sikkim: 8000-10000 ft., J.D. Hooker \& T. Thomson s.n. (Herb. Ind. Or. Hook. f. \& T. Thomson 55) (holotype: K[4]!; isotypes: BM!, C, CGE, FI, GH[2]!, L, P, W).

Symplocos wenshanensis M.S. Huang \& Y.F. Wu, Acta Phytotax. Sin. 24:199. 1986.
Symplocos yizhangensis Y.F. Wu, Acta Phytotax. Sin. 24:200. 1986.
Shrubs or trees, evergreen, to 10 m tall. Young branchlets glabrous or ferrugineous-tomentose; mature branchlets purplish; pseudo-terminal vegetative buds 3-6 mm, glabrous or ferrugineoustomentose. Petiole 6-12 mm, occasionally glandular; leaf blade narrowly oblong-elliptic, oblongoblanceolate, or oblanceolate, $8-18 \times 1.7-4.1 \mathrm{~cm}, 2.8-5.6$ times as long as wide, subcoriaceous, typically drying adaxially olive green to dark brown and abaxially dark green to brown, abaxially glabrous or sparsely ferrugineous to brown-tomentose when young but glabrescent, adaxially glabrous, midvein adaxially impressed, secondary veins $7-13$ on each side of midvein, base cuneate to slightly attenuate, margin serrulate to serrate and planar or slightly revolute, apex acuminate. Inflorescences axillary basally branched glomerules or simple compact spikes, $0.9-1.1 \mathrm{~cm}, 1-14$ flowered; rachis not evident. Bracts and bracteoles deltoid-ovate, nearly isomorphic but bracts slightly larger, $1.0-1.5 \times 1.2-2.0 \mathrm{~mm}$, persistent, ferrugineous-tomentose to nearly glabrous, margin entire and not glandular, apex acute to rounded. Pedicel absent. Hypanthium glabrous, subtending articulation present. Calyx limb gamosepalous for $0-0.2 \mathrm{~mm}$; lobes suborbicular to semi-elliptic, $1.0-1.5 \times 1.0-2.0 \mathrm{~mm}$, glabrous abaxially but margin frequently ferrugineous- to brown-tomentose and not glandular. Corolla white, 4-5 mm, membranous, gamopetalous only at base; lobes oblong, glabrous, adaxially smooth. Stamens ca. 20-35, adnate to corolla only at base, longest 7-9 mm ; filaments not abruptly constricted apically, smooth. Disk annular, glabrous. Style 4-5.5 mm, glabrous. Fruit blue, cylindrical to ellipsoid-cylindrical, $6-9 \times 2.5-3.5 \mathrm{~mm}$, glabrous; endocarp indurate throughout, 1 locule developed, perimeter $7-10$-ribbed. Seeds straight.

Symplocos glomerata is a very common species, growing within the middle elevations in Gaoligong Shan. It is the only one of the commonly encountered species of Symplocos with glomerules or compact spikes, the rachis being hidden by the rest of the inflorescence; the other common species (S. dryophila, S. ramosissima, and S. theifolia) have more elongate inflorescences with an evident rachis.

This species may not be distinct from Symplocos adenopus Hance. Symplocos glomerata supposedly differs from $S$. adenopus by a leaf blade margin with less than 6 glands (versus 6 to 12) per cm , but this character appears to vary continuously and may be clinal, with the variation ascribed to $S$. adenopus distributed to the east of Gaoligong Shan.

The inclusion of Symplocos heishanensis Hayata in Li et al. (2000) appears to be based on a misidentification of a specimen of S. glomerata (GLGS 1539).

Selected Illustrations.- R.F. Wu, Fl. Reipubl. Popularis Sin. 60(2):62 t. 22(17-20), 65 t. 23(8-10). 1987; G.H. Zhu, ed. Fl. China Ill. 15:t. 192(17-20), t. 193(8-10). 2000.

Phenology. - Fl. and fr. Feb-Oct.
Distribution and habitat.- Mixed evergreen and deciduous broadleaf forest, Subtropical evergreen broadleaf forest; 1300-2800 m. In GLGS: CHINA. Xizang. Yunnan: Fugong Xian (Lishadi Xiang, Shangpa Zheng), Gongshan Xian (Bingzhongluo Xiang, Cikai Zheng, Dulongjiang Xiang), Longling Xian (Longjiang Xiang), Longyang Qu (Lujiang Xiang), Lushui Xian (Gudeng Xiang, Pianma Xiang), Tengchong Xian (Dongshan Xiang, Guyong Zheng, Jietou Xiang, Puchuan Xiang, Qushi Xiang, Shangying Xiang, Wuhe Xiang), Yingjiang Xian. MYANMAR. Kachin: Myitkyina District (Chibyaw Township); Figure 10. Outside of GLGS: Fujian, N Guangdong, Hunan, Jiangxi, Xizang, Yunnan, Zhejiang [Bhutan, India, Sikkim].

Local name．－团花山矾 tuan hua shan fan
UsES．－Root used medicinally．
Additional specimens examined．－CHina．XIZANG： Buqiong Lake，SE Xizang， $1450 \mathrm{~m}, 15$ Nov 1992，H．Sun et al． 1372 （KUN）． YUNNAN：Shweli－Salween divide，7000－8000 ft．，Jun 1918，F 17628 （A，E， K，W［2］）；Shweli－Salween divide， 8000 ft．，Jul 1918，F 17655 （W）； 1933－1934，Tsai 55880 （A）；the first district，from Tong Yang to Xiong Ku， 2700 m， 6 Jun 1960，Wu 9280 （KUN）．FUGONG XIAN．Bijiang to Fa Du Feng， 5 Jun 1978，Nujiang Expedition 445 （KUN）；Lhuo－mo－geer， 2400 m， 1 Jan 1942，Wang 90588 （KUN）；Bi Jiang， 1 Jan 1942，Wang 90703 （KUN）． Lishadi Xiang．Between Shibali Logging Station and Yaping Pass，ca． 4.5 km W of Shibali，from the Nujiang to Yaping Pass，E side of Gaoligong Shan， 2884 m， 2 May 2004，GLGS 20241 （CAS）；between the Nujiang and Shibali Logging Station，ca． 16 km W of the Nujiang，from the Nujiang to Yaping Pass，E side of Gaoligong Shan， 2181 m， 7 May 2004，GLGS 20368 （CAS）． Shangpa Zheng．Qiao Mi Gu Lu， 2200 m， 8 Jun 1982，QX 7079 （KUN）； Qiao Mi Gu Lu， $2300 \mathrm{~m}, 8$ Jun 1982，QX 7095 （KUN）； $2500 \mathrm{~m}, 19$ Oct 1933， Tsai 54470 （A）； $2500 \mathrm{~m}, 20$ Oct 1933，Tsai 54529 （A）； $2800 \mathrm{~m}, 20$ May 1934， Tsai 58808 （A，KUN）； $2800 \mathrm{~m}, 20$ Oct 1934，Tsai 58847 （A，KUN）．GONG－ SHAN XIAN．W slope of Gaoligong Shan， $2400 \mathrm{~m}, 28$ Feb 1982，QX 8819 （KUN）；A Lu La Ka， 2500 m， 30 May 1960，Wu 9155 （KUN）．Bingzhongluo Xiang．Cha Pu Tong，2000－2307 m， 5 Sep 1940，Feng 7497 （KUN）；E slope of Gaoligong Shan， 2500 m， 1 Aug 1979，Nujiang Expedition 791252 （KUN）； Chinatung，Cham Pu Tung， $2300 \mathrm{~m}, 1$ Sep 1935，Wang 66613 （A，KUN，PE， PE）；Chi na tung，Cham pu tung， $2500 \mathrm{~m}, 1935-1936$ ，Wang 66662 （A，KUN， PE）；from Shan Ma to Bingzhongluo， $1700 \mathrm{~m}, 2$ May 1960，Wu 8766 （KUN）； Gongdan Holy Hills，E side of Gaoligong Shan，along the trail from Bingzhongluo to top of Holy Hills， 2540 m， 24 Apr 2002，GLGS 14672 （CAS， KUN）．Cikai Zheng．Qiqi，W side of Palehe River， 2040 m， 14 Oct 1996，


Figure 10．Distribution map of Symplocos glomerata in the GLGS region．

GLGS 7524 （E）；NE Qiqi Nature Reserve Station track heading towards Dulongjiang，margin of disturbed evergreen， 2150 m， 16 Oct 1996，GLGS 7705 （E）；Qiqi Nature Reserve Station，1900－2000 m， 19 Sep 1997， GLGS 9309 （E）；2－3 km along track from Qiqi towards Dongshaofang，2050－2200 m， 20 Sep 1997，GLGS 9387 （E）：E side of Gaoligong Shan，below Daxue Cao waterfall，along the Danzhu He on the rd from the Nu Jiang at Danzhu to the Myanmar border，2350－2470 m， 4 Jul 2000，GLGS 11972 （CAS，KUN）；loc．cit．，GLGS 11976 （CAS，KUN）；E side of Gaoligong Shan，W of Gongshan and W of Qiqi，along the Pula He on the trail to Dongshao Fang and Dulong Jiang Valley， 2250 m， 10 Jul 2000，GLGS 12255 （CAS，GH，KUN）；E side of Gaoligong Shan，W of Gongshan，along the Pula He on the trail from Qiqi to No． 12 Bridge and Dulong Jiang Valley， 2770 m， 30 Apr 2002，GLGS 14771 （CAS，KUN）；loc．cit．，GLGS 14775 （CAS，KUN）；E side of Gaoligong Shan，W of Gongshan，along the Pula He on the trail from Qiqi to No． 12 Bridge and Dulongjiang Valley， $2700 \mathrm{~m}, 3$ May 2002，GLGS 14864 （CAS，KUN）；E side of Gaoligong Shan at Km 28 on the rd from Gongshan to Kongdang， 2550 m， 13 Nov 2004，GLGS 22625 （CAS）；Heiwadi，E side of Gaoligong Shan， along the Pula He on the new rd to Dulong Jiang Valley， 1990 m， 17 May 2001，GLGS 13886 （CAS，KUN）； Qiqi， 2300 m .19 Jul 1982, QX 8201 （KUN）：Qiqi，2000－2100 m， 19 Jul 1982，QX 8212 （KUN）．Dulongjiang Xiang．Nengpula，directly opposite Bapo on the W side of the Dulong Jiang， $1400 \mathrm{~m}, 11 \mathrm{Dec} 1990$ ，GLGS 985 （CAS，KUN［2］）；Kongdang，on the E side of the Dulong Jiang， 1420 m， 30 Dec 1990，GLGS 1504 （CAS， KUN［2］）；Meiliwang， $1420 \mathrm{~m}, 30 \mathrm{Dec} 1991$ ，GLGS 1539 （KUN［2］）；Meiliwang， $1900 \mathrm{~m}, 10$ Jan 1991，GLGS 1935 （KUN［2］）：Meiliwang， 1900 m， 14 Jan 1991，GLGS 1949 （KUN［2］）；Songdangluo， 1560 m， 14 Jan 1991．GLGS 1994 （KUN［2］）：Xianjiudang，middle region of the Dulong Jiang Valley，ca． 8 km N of Kongdang on the E side of the Dulong Jiang， 1550 m． 22 Nov 1990，GLGS 2125 （CAS，KUN［2］）；loc．cit．，GLGS 2144 （CAS，KUN［2］）：Meiliwang，along the trail from Bapo to Gongshan on the E side of the Dulong Jiang， 2300 m， 16 Jan 1991．GLGS 3061 （CAS，KUN［2］）：along the Dandangwang He，NW of Bapo on the W side of the Dulong Jiang． 1380 m． 17 Jan 1991．GLGS 3204 （CAS，KUN［2］）；along the Dandangwang He，NW of Bapo
on the W side of the Dulong Jiang, 1600 m , 29 Jan 1991, GLGS 3680 (KUN [2]); along the Telawang He which is the southernmost tributary of the Dulong Jiang, S of Bapo on the E side of the Dulong Jiang, $1380 \mathrm{~m}, 31$ Jan 1991, GLGS 3845 (KUN [2]); along the Telawang He which is the southernmost tributary of the Dulong Jiang. S of Bapo on the E side of the Dulong Jiang, 1350 m, 31 Jan 1991, GLGS 3896 (KUN [2]); Maku, 2000 m. 8 Mar 1991, GLGS 4288 (KUN [2]); Maku, southern region of the Dulong Jiang Valley on the W side of the Dulong Jiang, $1950 \mathrm{~m}, 8$ Mar 1991, GLGS 4321 (CAS, KUN [3]); loc. cit., GLGS 4329 (KUN [2]); Mabidang, ca. 5 km N of Bapo on the E side of the Dulong Jiang, $1400 \mathrm{~m}, 8$ Mar 1991, GLGS 4635 (CAS, KUN [2]); E bank of Dulongjiang, $1500 \mathrm{~m}, 9$ Mar 1991, GLGS 4662 (KUN [2]); Kaladi, ca. 5 km SE of Bapo on the E side of the Dulong Jiang, $2350 \mathrm{~m}, 23$ Mar 1991, GLGS 4900 (KUN [2]); Qiawudang, S side of the Gamolai He, ca. 4 km SE of Bapo on the E side the Dulong Jiang, 2000 m , 25 Mar 1991, GLGS 5077 (KUN [2]); Lang Ben Dang, 2000 m, 27 Mar 1991, GLGS 5235 (KUN); Chawudang, 1850 m, 28 Mar 1991, GLGS 5278 (KUN [2]); Xuebalaka, ca. 7 km SE of Dizhengdang between Kongdang and Dizhengdang on the E side of the Dulong Jiang, $1850 \mathrm{~m}, 20$ Apr 1991, GLGS 6163 (KUN [2]); Xianjiudang, middle region of the Dulong Jiang Valley, ca. 8 km N of Kongdang on the E side of the Dulong Jiang, $1680 \mathrm{~m}, 27$ Apr 1991, GLGS 6595 (KUN [2]); Kongdang, $1550 \mathrm{~m}, 28$ Apr 1991, GLGS 6666 (KUN [2]); N of the second team, $2300 \mathrm{~m}, 16$ May 1991, GLGS 6801 (KUN [2]); loc. cit., GLGS 6802 (KUN [2]); loc. cit., GLGS 6819 (KUN [2]); Meiliwang, $2100 \mathrm{~m}, 20$ May 1991, GLGS 6911 (KUN [2]); W side of Gaoligong Shan, W of Gongshan, on the trail from Qiqi to Bapo in the Dulong Jiang Valley, 2050-2150 m, 17 Jul 2000, GLGS 12917 (CAS, KUN); near the Tibet-Burma border, Djiou-djiang (Irrawaddy or. sup.), 2400-2800 m, 9 Jul 1916, H.F. v. Handel-Mazzetti 9461 (A, W); Zhi Zhi Zu camping site, on the way from Gongshan to Dulongjiang, $2180 \mathrm{~m}, 9$ May 1979, Nujiang Expedition 79-68 (KUN); Qin Lang Dang, 1700 m, 12 Aug 1982, QX 9325 (KUN); Xian Jiu Dang, 1600 m , 23 Aug 1982, QX 9488 (KUN); Kong Dang to Xian Jiu Dang, 1600 m, 12 Aug 1982, QX 9497 (KUN). LONGLING XIAN. Longjiang Xiang. Xiaoheishan Provincial Preserve, Xiaotai Shan, Xiaoshui He, on W side of Gaoligong Shan, S of the new rd from Baoshan to Tengchong via Nankang Yakou, $2011 \mathrm{~m}, 21$ Aug 2003, GLGS 17271 (CAS, KUN); vicinity of Xiaoheshan, along trail on S side of hwy S317 (new hwy from Baoshan to Tengchong via Nankang Yakou) at km 23.5, W side of Gaoligong Shan, 2075 m, 24 May 2005, GLGS 24740; Xiaoshuihe, in Xiaoheishan, Provincial Nature Reserve area, 1990 m, 27 May 2005, GLGS 25064 (CAS). LONGYANG QU. Lujiang Xiang. Bawan Cun, Dasheyao, on E side of Gaoligong Shan along the old rd from Baoshan to Tengchong via Dahaoping, 2240 m, 2 Sep 2003, GLGS 18577 (CAS, KUN). LUSHUI XIAN. Cai Jia Ba, $2100 \mathrm{~m}, 25 \mathrm{Mar}$ 1989, H. Sun et al. 1654 (KUN). Gudeng Xiang. N'MaikhaSalween divide, 8000 ft ., May 1925, F 26574 (E, K, W). Pianma Xiang. Along the S bank of the Wuzhong River, W of Gulang Cun, between Pianma and Gangfang, W side of Gaoligong Shan, 1823 m, 14 May 2005, GLGS 24111 (CAS); Piansihe Village, 2050 m, 16 May 2005, GLGS 24299 (CAS). TENGCHONG XIAN. 6000 ft., Feb 1925, F 26241 (A, K). Dongshan Xiang. Hills S of Tengyuel, Feb 1925, 6000 ft., F 26241 (E). Guyong Zheng. Lang Ya Shan, 9 Apr 1980, D.Y. Xia B-22 (KUN); Lang Ya Shan, 9 Apr 1980, D.Y. Xia BG23 (KUN). Jietou Xiang. Shweli-Salween divide, 10000 ft., July 1917, F 15713 (A, E, K); Shweli-Salween divide, 8000 ft ., Aug 1919, F 18297 (A, E, K); Shweli-Salween divide, 7000-8000 ft., Apr 1924, F 24013 (E, K); Shweli-Salween divide, 7000-8000 ft., Apr 1924, F 24082 (E, K); Da Chuang Team, 2000 m, 9 Apr 1980, L.S. Xie 817 (KUN). Puchuan Xiang. Yang Lao Qing forest station, 1880-2020 m, 4 Oct 1960, W.C. Yin $60-$ 1339 (KUN). Qushi Xiang. Shweli-Salween divide, 7000-8000 ft., Apr 1914, F 12301 (BM); Shweli-Salween divide, 8000 ft., Jul 1918, F 17655 (A, E, K); Shweli-Salween divide, 8000 ft., Apr 1924, F 24007 (E, K). Shangying Xiang. Gaoligong Shan State Nature Reserve, top of ridge at border between Baoshan Shi and Tengchong Xian, N and S of the old rd from Baoshan to Tengchong via Dahaoping, $2400 \mathrm{~m}, 4$ Sep 2003, GLGS 18759 (CAS, KUN). Wuhe Xiang. Ridge at the pass of Daohaoping by following trail to the N of the pass, W side of Gaoligong Shan, $2432 \mathrm{~m}, 30$ May 2005, GLGS 25162 (CAS). YINGJIANG XIAN. From Yingjiang to Shuili, 1952, R. C. Ching 50247 (KUN). MYANMAR. KACHIN: MYITKYINA DISTICT. Chibyaw Township. 6 miles from Kangfang, 20 Feb 1939, Naw Mu Pa 15505 (K).
6. Symplocos laurina (Retzius) Wallich ex G. Don, Gen. Hist. 4:3. 1837. Basionym: Myrtus laurinus Retzius, Observ. Bot. 4:26. 1786. Eugenia laurina (Retzius) Willdenow, Sp. Pl., ed. 5, 2:967. 1799. Bobua laurina (Retzius) de Candolle, Prodr. 3:24. 1828. Symplocos spicata var. laurina (Retzius) C.B. Clarke in J.D. Hooker, Fl. Brit. Ind. 3:573. 1882. Dicalix laurinus (Retzius)

Migo, Bull. Shanghai Sci. Inst. 13:202. 1943. Symplocos cochinchinensis (Loureiro) S. Moore subsp. laurina (Retzius) Nooteboom, Leiden Bot. Ser. 1:156. 1975. Symplocos cochinchinensis var. laurina (Retzius) Nooteboom, Leiden Bot. Ser. 1:156. 1975. Type.- P. Hermann s.n. (holotype: P; isotype: L).

Decadia aluminosa Loureiro, Fl. Cochinchin. 1:315. 1790.
Symplocos loha Buchanan-Hamilton ex D. Don, Prodr. Fl. Nepal. 144. 1825.
Symplocos spicata Roxburgh var. zeylanica A. de Candolle, Prodr. 8:254. 1844.
Symplocos bodinieri Brand, Repert. Spec. Nov. Regni Veg. 3:217. 1906. Maesa aurea H. Léveillé, Repert.
Spec. Nov. Regni Veg. 10:375. 1912. Symplocos laurina var. bodinieri Handel-Mazzetti, Beih. Bot.
Centralbl. 62(B):34. 1943. Dicalix bodinieri (Brand) Migo, Bull. Shanghai Sci. Inst. 13:198. 1943.
Symplocos pinfaensis H. Léveillé, Repert. Spec. Nov. Regni Veg. 9:77. 1910.
Symplocos balfourii H. Léveillé, Repert. Spec. Nov. Regni Veg. 9:77. 1910.
Eurya cavaleriei H. Léveillé, Repert. Spec. Nov. Regni Veg. 9:450. 1911.
Maesa bodinieri H. Léveillé, Fl. Kouy-Tcheou 286. 1914.
Symplocos vinoso-dentata H. Léveillé, Bull. Acad. Int. Geogr. Bot. 24:283. 1914.
Trees, evergreen, to 16 m tall. Young branchlets and vegetative buds usually glabrous, rarely tawny brown-strigose; mature branchlets greenish; pseudo-terminal vegetative buds $3-11 \mathrm{~mm}$, glabrous or densely strigose. Petiole $0.5-1.7 \mathrm{~cm}$, glabrous, not glandular; leaf blade elliptic to slightly oblanceolate, $6.0-19.5 \times 1.7-5.4 \mathrm{~cm}, 2.2-4.3$ times as long as wide, subcoriaceous, typically drying yellowish green, both surfaces glabrous, midvein adaxially impressed, secondary veins $6-11(-13)$ on each side of midvein, base cuneate to rarely subrounded, margin serrulate to serrate and planar or slightly revolute, apex usually abruptly acuminate or occasionally acute to acuminate. Inflorescences pseudo-terminal and axillary simple or basally branched (rarely also more distally branched) spikes or racemes, $0.4-5.9 \mathrm{~cm}, 1-70$-flowered; rachis white- or ferrugineous-strigillose to -pilulose. Bracts and bracteoles ovate, nearly isomorphic but bracts slightly larger, 0.8-2.6 $\times$ $0.5-2 \mathrm{~mm}$, persistent, strigillose, margin often ciliate and rarely also glandular, apex acute to obtuse. Pedicel $0-2 \mathrm{~mm}$; bracteoles keeled, covering most or all of hypanthium. Hypanthium glabrous, subtending articulation present. Calyx limb not gamosepalous; lobes semi-orbicular, $0.5-1.2 \times 0.7-1.7 \mathrm{~mm}$, glabrous, margin entire and not glandular, apex rounded. Corolla white or yellow, $2.5-3.5 \mathrm{~mm}$, membranous, gamopetalous only at base; lobes oblong, glabrous, adaxially smooth. Stamens ca. 40 , adnate to corolla only at base, longest to 3.5 mm ; filaments not abruptly constricted apically, smooth. Disk annular, glabrous. Style $1.5-3 \mathrm{~mm}$, glabrous. Fruit blue to purple, ampulliform to globose, 4-7 $\times$ 3.5-6 mm, glabrous; endocarp indurate throughout, 1 locule developed, perimeter smooth. Seeds U-shaped.

Nooteboom $(1975,2003)$ has recognized this taxon as one of four subspecies under a broadly circumscribed species Symplocos cochinchinensis [i.e., as subsp. laurina (Retzius) Nooteboom]. Although in areas outside the Gaoligong Shan intermediates are apparent, possibly through extensive hybridization (Nooteboom 1996), we have not detected such intermediacy in the Gaoligong Shan and it thus seems best for the present purpose to here treat the two entities as species.

The inflorescences of both Symplocos laurina and S. cochinchinensis display a distinctive combination of characters (although they were found difficult to incorporate in the key): the inflorescence is often branched at the base, the rachis is stout and more or less rigid, and the pedicels are usually very short or more commonly lacking.

Selected Illustrations.- R.F. Wu, Fl. Reipubl. Popularis Sin. 60(2):59 t. 21(1-5, 11-13). 1987; G.H. Zhu, ed. Fl. China Ill. 15:t. 189(1-8). 2000.

Photographic image.- Figure 11.
Phenology. - Fl. Jun-Oct. fr. Oct-Jul.


Figure 11．Fruiting branch of Symplocos laurina．Photo by Lihua Zhou．
Distribltion and habitat．－Subtropical broadleaved evergreen forest； $1400-2800 \mathrm{~m}$ ．In GLGS：CHINA．Xizang：Zayü Xian．Yunnan：Gongshan Xian（Dulongjiang Xiang），Lianghe Xian （Pingshan Xiang），Longling Xian（Longjiang Xiang，Zhen＇an Zheng），Longyang Qu（Lujiang Xiang），Lushui Xian（Liuku Zheng），Tengchong Xian（Heshun Xiang，Jietou Xiang，Puchuan Xiang，Qushi Xiang，Shangying Xiang，Wuhe Xiang，Zhonghe Xiang）；Figure 12．Outside of GLGS：Xizang，Yunnan，Guizhou，Hunan，Guangxi，Guangdong，Fujian，Taiwan，Jiangsu，Zhejiang ［India，Japan，Myanmar，Sri Lanka；Pacific Islands］．

Local name．－黄牛奶树 huang niu nai shu
Additional specimens examined．－CHINA．XIZANG：ZAYÜ XIAN．Chayi， $2200 \mathrm{~m}, 16 \mathrm{Ju}$ 1973，QX $73-747$（KUN［2］）．YUNNAN：Oct 1918，F 17741 （A，E，K）；Oct 1918，F 17745 （A，E，K，W）． GONGSHAN XIAN．Dulongjiang Xiang．Kongdang，on the E side of the Dulong Jiang， $1420 \mathrm{~m}, 31 \mathrm{Dec}$ 1990，GLGS 1554 （CAS，KUN［2］）；Moqiewang， 1800 m ， 9 Jan 1990，GLGS 1758 （KUN［2］）；Meiliwang， along the trail from Bapo to Gongshan on the E side of the Dulong Jiang， $1900 \mathrm{~m}, 14$ Jan 1991，GLGS 1943 （CAS，KLN）；Moqiewang， $1800 \mathrm{~m}, 9$ Jan 1991，GLGS 1958 （KUN）；along the Dandangwang He，NW of Bapo on the W side of the Dulong Jiang， $1420 \mathrm{~m}, 17$ Jan 1991，GLGS 3202 （CAS，KUN［2］）；along the Dandangwang He，NW of Bapo on the W side of the Dulong Jiang， 1400 m， 19 Jan 1991，GLGS 3336 （KUN ［2］）；Maku，southern region of the Dulong Jiang Valley on the W side of the Dulong Jiang， $1900 \mathrm{~m}, 8$ Mar 1991，GLGS 4332 （CAS，KUN［2］）；Maku，southern region of the Dulong Jiang Valley on the W side of the Dulong Jiang， $1900 \mathrm{~m}, 8$ Mar 1991，GLGS 4345 （CAS，KUN［2］）．LIANGHE XIAN．Pingshan Xiang．Hills around Lung－Fau，8000－9000 ft．，Sep 1924，F 27436 （A，E，K）．LONGLING XIAN．Longjiang Xiang． Damahe Tang，Gucheng Shan，E side of Gaoligong Shan， $\mathbf{N}$ of the pass on the new rd from Baoshan to Tengchong via Nankang Yakou， 2100 m， 26 Aug 2003，GLGS 17968 （CAS，KUN）；Damahe Tang，Gucheng

Shan. E side of Gaoligong Shan, N of the pass on the new rd from Baoshan to Tengchong via Nankang Yakou, 2100 m, 26 Aug 2003, GLGS 17978 (CAS, KUN); Damahe Tang, Gucheng Shan, E side of Gaoligong Shan, N of the pass on the new rd from Baoshan to Tengchong via Nankang Yakou, 2100 m, 26 Aug 2003, GLGS 17984 (CAS, KUN); vicinity of Xiaoheshan, along trail on S side of hwy S317 (new hwy from Baoshan to Tengchong via Nankang Yakou) at km 23.5, W side of Gaoligong Shan, 2075 m, 24 May 2005, GLGS 24734 (CAS); Xiaoheshan Provincial Nature Reserve, S side trail at 23.5 km along hwy S317, $2075 \mathrm{~m}, 24$ May 2005, GLGS 24756 (CAS); Xiaoshuihe, in Xiaoheishan Provincial Nature Reserve area, 1990 m, 27 May 2005, GLGS 25070 (CAS). Zhen'an Zheng. Jieye Ba (Fern Leaf Dam), 2700 m, 1 Aug 1945, Wang 89869 (KUN). LONGYANG QU. Lujiang Xiang. Nankang Botany Garden (Lihuipo), summit of the Gaoligong Shan, 2130 m , 18 Nov 2000, GLGS 13202 (CAS, KUN); Nankang Botanical Garden (Lihuipo), 2150 m , 19 Nov 2000, GLGS 13283 (CAS, KUN); Lihuipo area near Nankang Village, E side of Gaoligong Shan near the crest of the range, just N of the new rd from Baoshan to Tengchong via Nankang Yakou, 2230 m, 23 Aug 2003, GLGS 17593 (CAS, KUN). LUSHUI XIAN. Liuku Zheng. Shweli-Salween divide, 8000-9000 ft., Jul 1924, F 24704 (E, K). TENGCHONG XIAN. Heshun Xiang. Jang-Jao Shan, Shweli-Salween divide, $7000-8000$ ft., Aug 1919, F 18480 (A, E, K). Jietou Xiang. Hillsides near Chii-Tung on the Teng Yueh-Talifu rd, 6000-7000 ft., Sep 1905, F 1095 (A, K); Shweli-Salween divide, 9000 ft., Jun 1917, F 15842 (A, E, K, KUN, W); Shweli-Salween divide, 10000 ft., Aug 1917, F 15844 (A, E, K, KUN, W); Shweli-Salween divide, 7000-8000 ft., Jun 1924, F 24401 (E, K); ShweliSalween divide, 8000 ft ., Sep 1924, F 25189 (E). Puchuan Xiang. The ninth district, $1880 \mathrm{~m}, 3$ Oct 1960, W.C. Yin 60-1280 (KUN). Qushi Xiang. ShweliSalween divide, 6000-7000 ft., Sep 1905, F 1037 (A, E, K); Shweli-Salween divide, 8000 ft ., Jun 1918, F 17491 (A, E, K); Shweli-Salween divide, 9000


Figure 12. Distribution map of Symplocos laurina in the GLGS region.
ft., Jun 1918, F 17522 (A, E). Shangying Xiang. Datianpo Cun, on the W side of Gaoligong Shan between Dahaoping and the pass dividing the Irrawaddy and Salween watersheds, on the old rd between Baoshan and Tengchong, $2170 \mathrm{~m}, 6$ Nov 1998, GLGS 11570-B (CAS, GH, KUN); small N-S valley in the Tangchang area above Dahaoping in the Gaoligong Shan State Nature Reserve. W side of Gaoligong Shan, SW of the old rd from Baoshan to Tengchong via Dahaoping, 2200 m. 2 Sep 2003, GLGS 18520 (CAS, KUN); loc. cit., GLGS 18525 (CAS, KUN); Tanchang area, 3.4 km above the forestry station at Dahaoping in the Gaoligong Shan State Nature Reserve, W side of Gaoligong Shan, on the old rd from Baoshan to Tengchong via Dahaoping, 2208 m, 3 Sep 2003, GLGS 18666 (CAS. KUN): from Longling to Tengchong 47 km , close to Shan Qing Forestry Station, $2000 \mathrm{~m}, 28$ Oct 1965, J.Z. Zhao 59 (KUN). Wuhe Xiang. Zhengding Cun, W side of Gaoligong Shan above the new rd from Baoshan to Tengchong via Nankang Yakou, $1830 \mathrm{~m}, 27$ Aug 2003, GLGS 18030 (CAS, KUN); Km 24.2 on hwy S 317, rd to Tenglang Village, Xiaodifang River drainage, W side of Gaoligong Shan, $2146 \mathrm{~m}, 27$ May 2005, GLGS 25028. Zhonghe Xiang. Flanks of volcanic mountain NW of Tengyueh, 7000, Jun 1912, F 8056 (E).
7. Symplocos oxyphylla Wallich ex A. de Candolle, Prodr. 8:256. 1844. Lodhra oxyphylla (Wallich ex A. de Candolle) Miers, J. Linn. Soc., Bot. 17:300. 1879. Type.- India Chattisgarh: Silhet, N. Wallich 4430 (holotype: G-DC; isotypes: BM, K, LE).

Symplocos pedicellata Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 42:89. 1873.
Trees, evergreen, to 6 m tall. Young branchlets glabrous; mature branchlets brown; pseudo-terminal vegetative buds ca. 9 mm . strigillose. Petiole $0.7-1.3 \mathrm{~cm}$, not glandular; leaf blade elliptic, $7-15 \times 3-5 \mathrm{~cm}, 2.6-2.7$ times as long as wide, chartaceous, drying green, both surfaces glabrous,
midvein adaxially impressed, secondary veins 6-9 on each side of midvein, base attenuate, margin nearly entire to crenulate and revolute, apex acute to acuminate. Inflorescences pseudo-terminal or axillary, basally branched racemes, to 4 cm , ca. 15-50-flowered; rachis white-strigillose. Bract caducous. Bracts and bracteoles deltoid, keeled, isomorphic, $0.5-0.9 \times 0.2-0.4 \mathrm{~mm}$, caducous or bracteoles persistent, strigillose at least medially, margin entire and not glandular, apex acute to acuminate. Pedicel $0-1.5 \mathrm{~mm}$; bracteoles covering less than half of hypanthium. Hypanthium glabrous, subtending articulation present. Calyx limb not gamosepalous; lobes broadly deltoid to semi-orbicular, $0.3-0.5 \times 0.5-0.6 \mathrm{~mm}$, glabrous or occasionally sparsely strigillose apical-medially, margin ciliolate, apex obtuse to rounded. Corolla white, 3-5 mm, membranous, gamopetalous only at base; lobes oblong-elliptic, glabrous, adaxially smooth. Stamens ca. 50, adnate to corolla only at base; filaments not abruptly constricted apically, smooth. Disk 5-glandular, thinly pilulose. Style ca. 3 mm , glabrous or basally pilulose. Fruit ovoid, ca. $9 \times 6 \mathrm{~mm}$, glabrous; endocarp indurate throughout, perimeter proximally longitudinally ribbed, conical beak smooth. Seeds straight, much lobed.


Figure 13. Symplocos oxyphila. - A. Flowering branch. - B. Leaf. - C. Flower. - D. Portion of opened corolla. - E. Flower with corolla and stamens removed showing remaining hypanthium, calyx, and gynoeceium.

As judged from the few specimens collected（Nooteboom 1975）， this species appears to be rare．It is known in Gaoligong Shan only from a single collection near the N＇mai Kha in Myanmar，although we have seen an additional collection from Tenasserim Division in southern Myanmar（J．Keenan et al．1709，A）．Neither of these spec－ imens have fruit；the description of the fruit here is therefore based on Nooteboom（1975）．It has apparently not been collected in the Gaoligong Shan since 1912.

Illustration．－Figure 13.
Phenology．－Fl．Sep．
Distribution and habitat．－700－800 m．In GLGS：MYAN－ MAR．Kachin：Myitkyina District．Chibyaw Township；Figure 14. Outside of GLGS：India，Myanmar，Thailand．

Local name．— 尖叶山砙（中文新名称）jian ye shan fan
Additional specimens examined．－MYANMAR．KACHIN： MYITKYINA DISTRICT．Chibyaw Township．Seniku－Laukhaung rd， 2500 ft ．， 24 Sep 1912，Mg Kyaw 50 （E）．

8．Symplocos paniculata（Thunberg）Miquel，Ann．Mus．Bot． Lugduno－Batavi 3：102．1867．Basionym：Prunus paniculata Thun－ berg in Murray，Syst．Veg．，ed．14．463．1784．Palura paniculata （Thunberg）Nakai，Trees Shrubs Japan 229．1922．Type．－Japan． C．P．Thunberg s．n．（holotype：UPS）．

Myrtus chinensis Loureiro，Fl．Cochinch．1：313．1790．Symplocos chinensis （Loureiro）Druce，Bot．Soc．Exch．Club Brit．Isles 4（suppl．2）：650． 1917. Palura paniculata var．chinensis（Loureiro）Nakai，Trees Shrubs Japan，


Figure 14．Distribution map of Symplocos oxyphila in the GLGS region Revis．Ed．310．1927．Palura chinensis（Loureiro）Koidzumi，Bot．Mag． （Tokyo）43：397．1929．Symplocos crataegoides Buchanan－Hamilton ex D．Don var．chinensis（Loureiro） Makino \＆Nemoto，Fl．Japan，ed．2，918． 1931.
Symplocos crataegoides Buchanan－Hamilton ex D．Don，Prodr．Fl．Nepal．145． 1825.
Symplocos hunanensis Handel－Mazzetti，Symb．Sinica 7：807． 1936.
Shrubs or trees，deciduous，to 7 m tall．Young branchlets glabrous or densely pubescent；mature branchlets grayish brown，dark reddish，or purplish；pseudo－terminal vegetative buds $2-3 \mathrm{~mm}$ ， glabrous．Petiole 1－9 mm，pubescent or occasionally glabrous，usually sparsely glandular；leaf blade broadly ovate，elliptic，oblong－elliptic，oblanceolate，oblong－oblanceolate，or obovate， $3.7-11.5 \times 1.5-6.8 \mathrm{~cm}, 1.4-2.8$ times as long as wide，chartaceous，typically drying abaxially gray－ ish green，green，or pale brown and adaxially green to brown，abaxially usually pubescent at least along midvein laterally and often throughout or rarely glabrous throughout，adaxially pubescent at least basally along midvein or rarely glabrous throughout，midvein adaxially impressed，secondary veins 4－6 on each side of midvein，base cuneate to slightly cordate，margin serrulate to denticulate， planar or slightly revolute，apex cuspidate，acuminate，or rarely rounded．Inflorescences pseudo－ter－ minal panicles with additional smaller panicles often present internodally（these often reduced to 1 or 2 flowers）and some leaves often bract－like，occasionally panicles borne directly on mature branchlets；pseudo－terminal panicle， $1-10 \mathrm{~cm}, 3$ to ca ． 100 －flowered；internodal panicles $0.4-3 \mathrm{~cm}$ ， $1-12$－flowered；rachis glabrous or pubescent．Bracts and bracteoles 0 or 1 per flower，linear，ovate， or lanceolate，isomorphic， $0.5-0.8 \times 0.1-1.5 \mathrm{~mm}$ or sometimes larger and leaf－like，caducous， glabrous or pubescent．margin often ciliate，glandular，or both，apex rounded to acuminate．Pedicel
$0.5-8 \mathrm{~mm}$. Bracteoles covering less than half of hypanthium. Hypanthium glabrous or pubescent, subtending articulation present. Calyx limb not gamosepalous; lobes semi-orbicular, oblong, or deltoid. $0.3-1.8 \times 0.5-1 \mathrm{~mm}$, abaxially glabrous or occasionally pubescent, margin ciliate, apex rounded to acuminate. Corolla white or pale yellow, 3-6.5 mm, membranous; lobes oblong, broadly elliptic. or ovate, glabrous, adaxially smooth. Stamens ca. 40-60, adnate to corolla only at base, longest 3-6 mm; filaments not abruptly constricted apically, smooth. Disk 5-lobed or low-annular, glabrous or pubescent. Style $2-3.5 \mathrm{~mm}$, glabrous. Fruit dark brown, blue, or black, ovoid to slightly pyriform. $4-8 \times 4-6.5 \mathrm{~mm}$. glabrous or pubescent; endocarp indurate throughout, 1 or 2 locules developed, perimeter smooth. Seeds U-shaped.

Symplocos paniculata is the only deciduous species of Symplocos in Gaoligong Shan (as well as Asia. S. tinctoria (Linnaeus) L'Héritier of the southeastern United States being the only other documented deciduous species in the genus). In cases where deciduousness is difficult to determine, the pseudo-terminal panicles of the species serve as an easy way to distinguish this species from others in Gaoligong Shan, being unique in the genus.

Selected Illustrations.- R.F. Wu, Fl. Reipubl. Popularis Sin. 60(2):73 t. 26(1-9). 1987; G.H. Zhu, ed. Fl. China Ill. 15:t. 195(1-9). 2000.

Photographic tmage.- Figure 15.
Phenology.- Fl. Apr-Jun, fr. Sep-Nov.
Distribution and habitat.- Disturbed or shrubby areas of subtropical broadleaved evergreen forest; 1200-1300 m. In GLGS: CHINA. Xizang: Zayü Xian (Tsarong Xiang). Yunnan: Gongshan Xian (Dulongjiang Xiang), Longling Xian, Tengchong Xian (Dongshan Xiang, Guyong


Figure 15. Fruiting branch of Symplocos paniculata. Photo by Lihua Zhou.

Zheng, Qingshui Xiang, Qushi Xiang, Wuhe Xiang), Yingjiang Xian (Tongbiguan Xiang). MYANMAR. Kachin: Putao District. (Khawbude Township); Figure 16. Outside of GLGS: Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hainan, Hebei, Heilongjiang, Henan, Hubei, Hunan, Jiangsu, Jiangxi, Jilin, Liaoning, Nei Mongol, Ningxia, Shaanxi, Shandong, Shanxi, Sichuan, Taiwan, Xizang, Yunnan, Zhejiang [Bhutan, India, Japan, Korea, Laos, Myanmar, Vietnam].

## Local name. - 白檀 bai tan

Additional specimens examined.- CHINA. XIZANG: ZAYÜ XIAN. Chayi, $2200 \mathrm{~m}, 26$ Jul 1973, QX 73-899 (KUN). Tsarong Xiang. Trulung, Po Tsangpo, Pome, 6500 ft., 25 May 1947, F. Ludlow 13033 (A). YUNNAN: $F 6797$ (K); May 1912, F 7883 (K); F 9842 (K); F 12748 (K); F $13880(\mathrm{~K}) ; F 13884(\mathrm{~K}) ; F 15027(\mathrm{~K}) ; 8000 \mathrm{ft} ., F 24023(\mathrm{~K})$. GONGSHAN XIAN. Dulongjiang Xiang. Taron-taru divide, valley of Bucahwang, 1700 m, 5 Nov 1958, J. Chen 239 (KUN). LONGLING XIAN. 1510 m, 30 Nov 1958, J. Chen 684 (KUN [2]); 1800 m, 9 Apr 1934, Tsai 55714 (KUN); 1800 m, 11 Apr 1934, Tsai 55729 (KUN [3]); 1800 m, 13 Apr 1934, Tsai 55775 (KUN). TENGCHONG XIAN. Dongshan Xiang. Qingcaitang, on the old rd from Tengchong to Baoshan between Tengchong and the Longchuan Jiang, 1860 m, 2 Nov 1998, GLGS 11369 (CAS, GH, KUN [2]). Guyong Zheng. Heinitang, Houqiao, 1600 m, 17 Apr 1985, Fragrance Resources Expedition 277 (KUN [3]); Houqiao, Guyong River bank, 1680 m, Wu 6830 (KUN [2]). Qingshui Xiang. Rehai Hot Spring ca. 10 km SW of Tengchong, $1500 \mathrm{~m}, 24$ Oct 1998, GLGS 10888 (CAS, GH, KUN). Qushi Xiang. Daba, 1900 m, 18 May 1997, Z.L. Dao et al 9478 (KUN [2]); Jiangzuo, 1930 m, 12 Sep 1960, W.C. Yin 1012 (KUN [2]); $1930 \mathrm{~m}, 21$ Sep 1960, W.C. Yin 1227 (KUN [2]); Daba. Dashuijing, 2050 m, 9 Sep 1995, S.X. Yang 831 (KUN [2]). Wuhe


Figure 16. Distribution map of Symplocos paniculata in the GLGS region. Xiang. Huangcaoling area, near Zhengding Village, W side of Gaoligong Shan on the new rd from Baoshan to Tengchong via Nankang Yakou, 1900 m, 26 Aug 2003, GLGS 17937 (CAS, KUN). Zhonghe. Margin of lava bed W of Tengyueh, 5000 ft ., May 1912, $F 7457$ (K). YINGJIANG XIAN. Kachangcaoba Village, 1240 m, 10 Apr 1985, Fragrance Resources Expedition 210 (KUN [2]). Tongbiguan Xiang. $1350 \mathrm{~m}, 8$ Apr 1985, Fragrance Resources Expedition 125 (KUN [2]); Shibie Village, 1350 m, 8 Apr 1985, Fragrance Resources Expedition 145 (KUN [2]). MYANMAR. KACHIN: PUTAO DISTRICT. Khawbude Township. SalweenKiu Chiang divide, 9000 ft ., Oct 1924, F 25665 (E), F 25889 (E).
9. Symplocos pendula Wight, Icon. Pl. Ind. Orient. 4:11. 1848. Palura pendula (Wight) Miers, J. Linn. Soc., Bot. 17:297. 1879. Cordyloblaste pendula (Wight) Alston in Trimen, Handb. Fl. Ceylon 6(6):188. 1931. Types.- India: Pulney Mts., Herb. Wight 2136 (syntype: K; isosyntypes: E, L); SRI LANKA. Herb. Wight s.n. (syntype: K).

Symplocos confusa Brand in Engler, Pflanzenr. 6(IV. 242):88. 1901. Bobua confusa (Brand) Kanehira \& Sasaki in Sasaki, List Pl. Formosa 330. 1928. Cordyloblaste confusa (Brand) Ridley, Fl. Malay. Penins. 2:307. 1923.

Symplocos punctulata Masamune \& Syozi, Acta Phytotax. Geobot. 12:201. 1950.
Shrubs or trees, evergreen, to 6 m tall. Young branchlets glabrous, hirtellous-tomentellous, or sparsely pilulose: mature branchlets grayish brown; pseudo-terminal vegetative buds $3-5 \mathrm{~mm}$, strigillose. Petiole $0.7-1.6 \mathrm{~cm}$, not glandular; leaf blade elliptic to obovate, $8.3-11.5 \times 3.5-5.0 \mathrm{~cm}$, 1.9-2.9 times as long as wide. subcoriaceous. drying grayish green to brown, abaxially glabrous,
adaxially glabrous or occasionally white－puberulent along midvein，midvein adaxially impressed， secondary veins $8-12$ on each side of midvein，base subrounded to cuneate and often slightly atten－ uate，margin entire，shallowly crenate，or slightly undulate and slightly revolute，apex rounded to acuminate．Inflorescences pseudo－terminal or axillary，raceme－like cymes， $1-1.7 \mathrm{~cm}, 1-7$－flowered； rachis tawny－to ferrugineous－strigillose to－hirtellous；bract deltoid to linear， $1.2-1.8 \times 0.8-1 \mathrm{~mm}$ ， apex acute to obtuse．Bracts and bracteoles caducous or persistent，strigillose，margin hirtellous and not glandular．Pedicel $1.5-5 \mathrm{~mm}$ ；bracteoles triangular， $0.5-0.8 \times 0.2-0.8 \mathrm{~mm}$ ，covering less than half of hypanthium，apex acute．Hypanthium white to tawny－strigillose，subtending articulation absent．Calyx limb gamosepalous for ca． $1-1.5 \mathrm{~mm}$ ；lobes low－hemispheric， $0.4-1.1 \times 1-1.8 \mathrm{~mm}$ ， strigillose at least medially，margin ciliate and not glandular，apex rounded to often nearly truncate． Corolla white， $0.5-1.5 \mathrm{~cm}$ ，fleshy，gamopetalous ca．half the total length；lobes spatulate，abaxially usually pubescent，adaxially papillose．Stamens ca． $30-50$ ，longest $3-15 \mathrm{~mm}$ ，adnate to corolla for ca ．half the total length，connate distally beyond corolla adnation for $3-5 \mathrm{~mm}$ ，distalmost portions distinct for $1-3.5 \mathrm{~mm}$ ；filaments abruptly constricted apically，longest distinct portions erect，short－ est down－curved．Disk cylindrical，prominent，apex at least sparsely hirtellous．Style $4-15 \mathrm{~mm}$ ， glabrous or densely hirtellous to hirsute．Fruit fusiform， $10-15 \times 3-6 \mathrm{~mm}$ ，strigillose；endocarp indurate throughout， 2 or 3 locules developed，perimeter smooth． Seeds straight．

Selected Illustrations．－R．F．Wu，Fl．Reipubl．Popularis Sin．60（2）：76 t．27（1－8）．1987；G．H．Zhu，ed．Fl．China Ill．15：t． 196（1－8）． 2000.

Phenology．－Fl．Jun－Aug，fr．Sep－Nov．
Distribution and habitat．－Broadleaved forest；ca． 1200 m ． In GLGS：CHINA．Yunnan：Gongshan Xian（Dulongjiang Xiang）， MYANMAR．Kachin：Myitkyina District（Saulot Township）；Figure 17．Outside of GLGS：Fujian，Guangdong，Guangxi，Guizhou，S Hainan，Hunan，Jiangxi，Taiwan，Yunnan，Zhejiang［India，Indonesia， Japan，Malaysia，Myanmar，Vietnam］．

Local name．－吊钟山矾 diao zhong shan fan
Symplocos pendula is one of two species comprising Symplocos subgenus Cordyloblaste（Henschel ex Moritzi）Gamble，the first－ diverging clade in the genus（Wang et al．2004；Fritsch et al．2006； Fritsch and Almeda，in press）．The other species［S．henschelii （Moritzi）Bentham ex C．B．Clarke）］ranges from Southeast Asia to Malesia．

Additional specimens examined．－CHINA．YUNNAN： GONGSHAN XIAN．Dulongjiang Xiang．Salween－Kiu Chiang divide， 10000 ft ．，Aug 1924，F 25758 （E，K）；the 4th village，Miliwaluo， $1200 \mathrm{~m}, 12$ Nov 1959，Feng 24211 （KUN［2］）；Kongdang， 1550 m， 28 Apr 1991，GLGS 6658 （KUN［2］）；Longyuan， 1900 m， 29 Aug 1982，QX 9742 （KUN）；Taron－ taru divide，valley of Bucahwang， $1500 \mathrm{~m}, 6$ Sep 1959，Yü 24211 （KUN）． MYANMAR．KACHIN：MYITKYINA DISTRICT．Saulot Township． Hills around Htawgaw， 7000 ft．，Sep 1924，F 25073 （E，K）．


Figure 17．Distribution map of Symplocos pendula in the GLGS region．

10．Symplocos racemosa Roxburgh，Fl．Ind．ed．1832，415．1832．Symplocos racemosa var． composita Kurz，J．Asiat．Soc．Bengal，Pt．2，Nat．Hist．46：238．1877．Type．－India．West Bengal： Burdwan and Midnapore，W．Roxburgh s．n．（lectotype［designated by Nooteboom 1975］：P）．

Symplocos rigida Wallich ex G．Don，Gen．Syst．4：3．1837．Symplocos racemosa var．roxburghiana Kurz，J．
Asiat．Soc．Bengal，Pt．2，Nat．Hist．46：238． 1877.
Symplocos leucantha Kurz，J．Asiat．Soc．Bengal，Pt．2，Nat．Hist．42：89． 1873.
Symplocos intermedia Brand，Repert．Spec．Nov．Regni Veg．3：217． 1906.
Symplocos macrostachya Brand，Pflanzenr．6（IV．242）：36 1901.
Symplocos macrostachya var．leducii Brand，Repert．Spec．Nov．Regni Veg．3：217． 1906.
Shrubs or trees，evergreen，to 12 m tall．Young branchlets yellow－pilose；mature branchlets grayish；pseudo－terminal vegetative buds $2-6(-8) \mathrm{mm}$ ，yellow－to ferrugineous－sericeous to－lanate． Petiole $4-15 \mathrm{~mm}$ ，not glandular；leaf blade elliptic to ovate－elliptic， $9.2-12.5 \times 3.2-5.5 \mathrm{~cm}, 2.1-3.0$ times as long as wide，chartaceous to subcoriaceous，typically drying abaxially pale green and adax－ ially green to dark green，abaxially sparsely yellow－strigose－pilose at least on midvein or rarely glabrous，adaxially yellow－pilose to－pilulose on midvein or rarely glabrous，midvein adaxially impressed，secondary veins $7-11$ on each side of midvein，base rounded to broadly cuneate and occasionally slightly attenuate，margin crenulate－serrulate to nearly entire，planar or slightly revo－ lute，apex acute to obtuse．Inflorescences pseudo－terminal，or axillary，simple or rarely branched racemes， $2.5-7.2 \mathrm{~cm}, 4-22$－flowered；rachis yellow－to ferrugineous－lanate－villous．Bracts and bracteoles broadly ovate to suborbicular，often keeled，isomorphic but bracts larger， $2-4 \times 1-2.5$ mm ，caducous，strigose to sericeous，margin lanulate and often glandular，apex acute．Pedicel 1－3 mm ；bracteoles covering less than half of hypanthium．Hypanthium glabrous，subtending articula－ tion present．Calyx limb gamopetalous for $0.3-0.5 \mathrm{~mm}$ ；lobes broadly semi－oblong，ovate，or sub－ orbicular， $1.3-1.8 \times 1.2-1.8 \mathrm{~mm}$ ，glabrous or medially strigose，mar－ gin entire，ciliolate，or lanulate，apex rounded to obtuse．Corolla white， $3.5-5 \mathrm{~mm}$ ，membranous，gamopetalous only at base；lobes oblong－elliptic to oblong－ovate，glabrous，adaxially smooth．Stamens ca．60－100，adnate to corolla only at base，longest $4.5-7 \mathrm{~mm}$ ；fila－ ments not abruptly constricted apically，smooth．Disk annual－pentag－ onal to 5－lobed，villous．Style $1-4 \mathrm{~mm}$ ，glabrous or villous toward base．Fruit blue，ellipsoid－cylindrical，5－11 $\times 3-5 \mathrm{~mm}$ ，glabrous； endocarp indurate throughout， 3 locules developed，perimeter smooth or ca． $8-10$－ribbed．Seeds straight．

Selected Illustrations．－R．F．Wu，Fl．Reipubl．Popularis Sin． $60(2): 44$ t．16（5－－9）．1987；G．H．Zhu，ed．Fl．China Ill．15：t． 186（5－9）． 2000.

Phenology．－Fl．Sep－Dec，fr．May－Jul of following year．
Distribution and habitat．－Mixed forests，subtropical ever－ green broadleaf forest； $1100-1200 \mathrm{~m}$ ；In GLGS：CHINA．Yunnan： Longling Xian（Zhen＇an Zheng），Lushui Xian（Gudeng Xiang）， Tengchong Xian（Guyong Xiang），Yingjiang Xian（Tongbiguan Xiang）；Figure 18．Outside of GLGS：Guangdong，Guangxi，Hainan， SW Sichuan，Yunnan［India，Myanmar，Thailand，Vietnam］．

LOCAL NAME．－吊钟山矾 zhu zhi shu
Additional specimens examined．－CHINA．YUNNAN： LONGLING XIAN． $1600 \mathrm{~m}, 30$ Sep 1933，Tsai 56679 （A）．Zhen＇an Zheng． Zhuging Village， 5 km from Longling three ways crossing， $1190 \mathrm{~m}, 28$ May 2005．GLGS 23917 （CAS）．LUSHUI XIAN． 1400 m .30 Sep 1933，Tsai 54551 （A，KUN）．Gudeng Xiang．N＇Maikha－Salween divide， 8000 ft ．，Jul 1919，F 18234 （A，E，K，W）．TENGCHONG XIAN．Guyong Zheng．


Figure 18．Distribution map of Symplocos racemosa in the GLGS region．

Between Tengyueh and Burmese border, en route to Sadon, 1 Nov 1922, Rock 7324 (A). YINGJIANG XIAN. Tongbiguan Xiang. Between Tengyueh and Bhamo, 1 Nov 1922, Rock 7845 (A).

Symplocos racemosa has apparently been collected only once since 1933, in 2005 (GLGS 23917). This specimen is only in young bud. Collection of a representative from this population in fertile condition would solidify its identification.
11. Symplocos ramosissima Wallich ex G. Don, Gen. Hist. 4:3. 1837. Type.- Nepal. Sheopore, year 1821, T. Thomson s.n. (N. Wallich Cat. No. 4425) (holotype: K!; isotypes: BM, C, CGE, E[2]!, FI, G-DC, GH!, L, LE, NY, W).

Symplocos fasciculata Zollinger var. chinensis Brand, Repert. Spec. Nov. Regni Veg. 3:217. 1906.
Symplocos stapfiana H. Léveillé, Repert. Spec. Nov. Regni Veg. 9:444. 1911.
Symplocos myriantha Rehder in Sargent, Pl. Wilson. 2:596. 1916. Dicalix myrianthus (Rehder) Migo, Bull. Shanghai Sci. Inst. 13:203. 1943.
Symplocos ramosissima var. salweenensis Handel-Mazzetti, Symb. Sin. 7:808. 1936.
Symplocos stapfiana var. leiocalyx Handel-Mazzetti, Beih. Bot. Centralbl. 26(B):26. 1943.
Trees, evergreen, to 12 m tall. Young branchlets glabrous or ferrugineous-strigose; mature branchlets purplish to brownish; pseudo-terminal vegetative buds $4-8 \mathrm{~mm}$, proximally ferrugi-neous- to brown- tomentose, pubescence extending onto distal portion of mature branchlet, sericeous at least along distal portion of outer scale midvein. Petiole $5-12 \mathrm{~mm}$, often minutely sparsely glandular, glands caducous; leaf blade elliptic to slightly oblanceolate, $6.4-11.4 \times 1.7-3.7$ $\mathrm{cm}, 1.9-4.5$ times as long as wide, chartaceous, typically drying green to pale brown, abaxially glabrous or white-strigose proximally along midvein and rarely on surface, adaxially often minutely white-hispidulous proximally along midvein or occasionally glabrous, midvein adaxially impressed, secondary veins $6-10$ on each side of midvein, base cuneate to subrounded, margin crenulate-serrulate and planar or slightly revolute, apex long-acuminate. Inflorescences simple or occasional basally branched spikes or racemes, $1-4.5 \mathrm{~cm}, 1-20$-flowered, often produced on proximal leafless regions of branchlets; rachis white- or pale ferrugineous-puberulent or occasionally glabrous; bract usually caducous. Bracts and bracteoles $\pm$ deltoid, $\pm$ isomorphic but bracts somewhat larger, $0.4-3.2 \times 0.4-1.2 \mathrm{~mm}$, sparsely strigillose especially on midvein or glabrous, margin ciliate and occasionally glandular, apex acute. Proximal pedicels $0-2 \mathrm{~mm}$, distal pedicels usually shorter or absent; bracteoles usually persistent, covering less than half of hypanthium. Hypanthium strigillose or rarely glabrous, subtending articulation present. Calyx limb not gamopetalous; lobes broadly ovate to more often hemispherical, $0.6-1 \times 0.9-1.3 \mathrm{~mm}$, glabrous or sparsely strigillose, margin ciliate and not glandular, apex broadly obtuse to rounded. Corolla white or pale yellow, 3-5 mm , membranous, gamopetalous only at base; lobes oblong, glabrous, adaxially smooth. Stamens $50-70$, adnate to corolla only at base, longest 4-5.5 mm; filaments not abruptly constricted apically, smooth. Disk $\pm 5$-lobed, glabrous. Style $3-4.5 \mathrm{~mm}$, glabrous. Fruit ellipsoid, $7-11 \times 4-6 \mathrm{~mm}$, strigillose, puberulent, or rarely glabrous; endocarp indurate throughout, 1 locule developed, perimeter smooth. Seeds straight.

Symplocos ramosissima is one of the most common species of Symplocos in Gaoligong Shan, often forming subdominant stands in the forest understory where there are sufficient light gaps, or along forest edges. The white flowers have been observed to be highly attractive to bees, and individuals appear to fruit in abundance.

Selected Illustrations.— R.F. Wu, Fl. Reipubl. Popularis Sin. 60(2):38 t. 149(6-9). 1987; G.H. Zhu, ed. Fl. China Ill. 15:t. 183(6-9). 2000.

Photographic images.- Figures 19-20.


Figure 19．Flowering branch of Symplocos ramosissima．Photo by M．Dickson．
Phenology．－Fl．Apr－Aug，fr．Aug－Oct．
Distribution and habitat．－Subtropical broadleaved evergreen forest；1600－2900 m．In GLGS：CHINA．Xizang：Zayü Xian（Tsarong Xiang）．Yunnan：Fugong Xian（Lumadeng Xiang， Shangpa Zheng）．Gongshan Xian（Bingzhongluo Xiang．Cikai Zheng，Dulongjiang Xiang）， Longling Xian（Longjiang Xiang，Zhen｀an Zheng），Longyang Qu（Bawan Xiang，Lujiang Xiang， Mangkuan Xiang），Lushui Xian（Chen｀gan Xiang，Pianma Xiang），Tengchong Xian（Guyong Xiang．Jietou Xiang．Mingguang Xiang．Puchuan Xiang，Qushi Xiang，Shangying Xiang，Wuhe Xiang），MYANMAR．Kachin：Myitkyina District（Saulot Township），Putao District（Khawbude Township）；Figure 21．Outside of GLGS：Guangdong．Guangxi，Guizhou，Hubei，Hunan，Sichuan， Xizang，Yunnan［Bhutan，India，Myanmar，Nepal，Vietnam］．

Local name．－多花山砙 duo hua shan fan
Additional speciniexs extiined．－CHINA．XIZANG：ZAYÜ XIAN．Tsarong Xiang．Salween－ Kiu Chiang divide．W of Chamatong， 10000 ft ．，Jun 1922，F 21798 （A，E，K，W）．YUNNAN：F 16083 （A，K）； F 17606 （A，K）．FUGONG XIAN．Lumadeng Xiang．Yaping Cun．above old Shibali on the N side of S fork of Yamu He．E side of Gaoligong Shan． 2700 m． 21 Aug 2005，GLGS 28824 （CAS）．Shangpa Zheng． Pumigulu． 1700 m .7 May 1982．Nujiang Expedition 7040 （KUN）．GONGSHAN XIAN．Doyonlumba at Salween River．2500－2900 m． 1 Aug 1916，H．F．ı：Handel－Mazzetti 9604 （W）．Bingzhongluo Xiang．Der－la， Champutung． 1 Oct 1936．Hang 66890 （A．PE）．Cikai Zheng．NE of Qiqi Nature Reserve Station，track head－ ing towards Dulongjiang．2000－2500 m． 20 Sep 1997．GLGS 7590 （E［2］）；2－3 km along track from Qiqi towards Dongshaofang．2050－2200 m． 19 Sep 1998．GLGS 9340 （E）：2－3 km along track from Qiqi towards Dongshaofang．2050－2200 m． 20 Sep 1997．GLGS 9407 （E）：Qiqi． 2000 m .18 Jul 1982，QX 8113 （KUN）； Qiqi， 2000 m .19 Jul 1982．QX 8168 （KUN）．Dulongjiang Xiang．Kaladi．ca． 5 km SE of Bapo on the E side of the Dulong Jiang． 2300 m .23 Mar 1991．GLGS 7859 （CAS．KUN）：along the Wangmei He，N of the trail


Figure 20. Fruiting branch of Symplocos ramosissima. Photo by M. Dickson.
from Bapo to Gongshan and NW of Xishaofang on the E side of the Dulong Jiang, $2200 \mathrm{~m}, 26$ Mar 1991, GLGS 5205 (KUN [2]); the second team, $2100 \mathrm{~m}, 20$ May 1991, GLGS 6898 (KUN); $2200 \mathrm{~m}, 27$ Jul 1982, QX 8688 (KUN). LONGLING XIAN. Longjiang Xiang. Xiaoheishan Provincial Preserve, Xiaotai Shan, Xiaoshui He, on W side of Gaoligong Shan, S of the new rd from Baoshan to Tengchong via Nankang Yakou, 2011 m, 21 Aug 2003, GLGS 17319 (CAS, KUN); Damahe Tang, Gucheng Shan. E side of Gaoligong Shan, N of the pass on the new rd from Baoshan to Tengchong via Nankang Yakou, $2100 \mathrm{~m}, 26$ Aug 2003, GLGS 17971 (CAS, KUN); W side of Nankang Pass, 2181 m, 27 May 2005, GLGS 23808 (CAS); vicinity of Xiaoheshan, along trail on S side of hwy S317 (new hwy from Baoshan to Tengchong via Nankang Yakou) at km 23.5, W side of Gaoligong Shan, 2037 m, 23 May 2005, GLGS 24616 (CAS). Zhen'an Zheng. 1830-2340 m, 4 Dec 1958, J. Chen 735 (KUN); Nankang Pass, 2170 m, 26 May 2005, GLGS 23726 (CAS); loc. cit., GLGS 23755 (CAS); loc. cit., GLGS 23759 (CAS). LONGYANG QU. BAWAN. Ca. 1.5 direct km SE of E Nankang Yakou on the rd from Baoshan to Tengchong, E side of Gaoligong Shan, 2181 m, 27 May 2005, GLGS 23803 (CAS); trail N of hwy S317 (rd from Baoshan to Tengchong) starting at km 22.6 Lihuipo, E side of Gaoligong Shan, 2167 m, 23 May 2005, GLGS 24641 (CAS). Lujiang Xiang. Nankang Botany Garden (Lihuipo), summit of the Gaoligong Shan, $2050 \mathrm{~m}, 16$ Nov 2000, GLGS 13072 (CAS, KUN); Nankang Botany Garden (Lihuipo), summit of the Gaoligong Shan, $2100 \mathrm{~m}, 17$ Nov 2000, GLGS 13161 (CAS, KUN); Lihuipo area near Nankang Village, E side of Gaoligong Shan near the crest of the range, just N of the new rd from Baoshan to Tengchong via Nankang Yakou, 2230 m, 23 Aug 2003, GLGS 17558 (CAS, KUN); Lihuipo area
near Nankang Village, E side of Gaoligong Shan near the crest of the range, just N of the new rd from Baoshan to Tengchong via Nankang Yakou, 2210 m, 24 Aug 2003, GLGS 17725 (CAS, KUN); Weihuipo area, near Nankang Village, E side of Gaoligong Shan, $S$ of Nankang Yakou on the new rd from Baoshan to Tengchong via Nankang Yakou, 2180 m, 26 Aug 2003, GLGS 17896 (CAS, KUN). Mangkuan Xiang. Hanlong, Baihualing Village, 1650 m, 2 Jun 2005, GLGS 25338 (CAS). LUSHUI XIAN. CHEN'GAN. N'Maikha-Salween divide, 9000 ft., Jun 1925, F 26842 (A, E, W); W flank of the N'Maikha-Salween divide, 7000-8000 ft., Jul 1925, F 27104 (A, E, K, W); W flank of the N'Maikha-Salween divide, Oct 1925, F 27307 (A, E). Pianma Xiang. 2700 m, 8 Aug 1978, Nujiang Expedition 1814 (KUN); 2800 m, 13 Jul 1964, Wu 8022 (KUN); 2520 m, 17 Jul 1964, Wu 8105 (KUN); 2400 m, 31 Jul 1964, Wu 8290 (KUN). TENGCHONG XIAN. Guyong Zheng. Lang Ya Shan, 13 Apr 1980, D.Y. Xia BG-32 (KUN). Jietou Xiang. Shweli-Salween divide, 9000 ft., Jul 1917, F 15716 (A, E, K); F 15739 (A, K, W); Shweli-Salween divide, 9000 ft., Aug 1917, F 15904 (A, E, K, W); Shweli-Salween divide, 8000 ft ., Jun 1919, F 17629 (A, E, K); F 18031 (A, E, K); 7000-8000 ft., May 1924, F 24180 (E, K); 8000 ft., Jun 1924, F 24402 (E, K); Shweli-Salween divide, 8000 ft., Jun 1924, F 24372 (E, K); ShweliSalween divide, 9000 ft ., Jun 1924, F 24678 (E, K, W); Shweli Salween divide, 8000 ft ., Sep 1924, F 25159 (E, K). Shaba Cun, community forest of Lidazhai, W side of Gaoligong Shan, 2280 m, 23 Dec 2000, GLGS 13648 (CAS, KUN). Puchuan Xiang. The ninth district, 1880-2020 m, 3 Oct 1960, W.C. Yin 60-1296 (KUN). Qushi Xiang. Daba, 2400 m, 17 May 1997, Z.L. Dao et al 9473 (KUN [3]); Shweli-Salween divide, 9000 ft ., May 1919, F 17889 (E, K). Shangying Xiang. Qiaojie Cun in vicinity of Henghe Village, W side of Gaoligong Shan on the old rd from Baoshan to Tengchong via Dahaoping, 2230 m, 1 Sep 2003, GLGS 18365 (CAS, KUN); small N-S valley in the Tangchang area above Dahaoping in the Gaoligong Shan State


Figure 21. Distribution map of Symplocos ramosissima in the GLGS region. Nature Reserve, W side of Gaoligong Shan, SW of the old rd from Baoshan to Tengchong via Dahaoping, 2080 m, 2 Sep 2003, GLGS 18473 (CAS, KUN); Gaoligong Shan State Nature Reserve, Taipingpu area, W side of Gaoligong Shan on the old trail (southern silk rd) just N and above the old rd from Baoshan to Tengchong via Dahaoping. 2300 m, 4 Sep 2003, GLGS 18694 (CAS, KUN); Gaoligong Shan State Nature Reserve, top of ridge at border between Baoshan Shi and Tengchong Xian, N and S of the old rd from Baoshan to Tengchong via Dahaoping, 2400 m, 4 Sep 2003, GLGS 18780 (CAS, KUN); on the way from Baoshan to Tengchong, 50 km along old rd, $2050 \mathrm{~m}, 30$ May 2005, GLGS 25212 (CAS); 47 km along old Baoshan to Tengchong rd, Dahaoping, $2200 \mathrm{~m}, 30$ May 2005, GLGS 26053 (CAS); loc. cit., GLGS 26061 (CAS). Wuhe Xiang. Ridge $S$ of the pass at the top of Gaoligong Shan on the old rd from Baoshan to Tengchong via Dahaoping, W side of Gaoligong Shan, $2525 \mathrm{~m}, 5$ Sep 2003, GLGS 18848-A (CAS, KUN); Lihuipo, Damatang River, 2190 m, 26 May 2005, GLGS 24929 (CAS); above Dahaoping along the ridge S of Dahaoping Yakou (pass at the border between Tengchong Xian and Longyang Qu), W side of Gaoligong Shan, $2405 \mathrm{~m}, 30$ May 2005, GLGS 25119 (CAS); ridge at the pass of Daohaoping by following trail to the N of the pass, W side of Gaoligong Shan, $2432 \mathrm{~m}, 30$ May 2005, GLGS 25179 (CAS). MYANMAR. KACHIN: MYITKYINA DISTRICT. Saulot Township. Htawgaw Bum, N of Htawgaw, $7000 \mathrm{ft} .$. , Jun 1924, F 24589 (E, K, W). PUTAO DISTRICT. Khawbude Township. Salween-Kiu Chiang divide, 9000 ft ., Jun 1924, F 25653 (E).
12. Symplocos sulcata Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 46:65. 1870. Symplocos macrophylla Wallich ex A. de Candolle var. sulcata (Kurz) Nooteboom, Leiden Bot. Ser. 1:231. 1975. Type.- Myanmar. Mon: Martaban, Daunat Pass, 4000 ft ., D. Brandis s.n. (holotype: ?CAL).

Symplocos yunnanensis Brand in Engler，Pflanzenr．6（IV．242）：68．1901．Dicalix yurnanensis（Brand）Migo， Bull．Shanghai Sci．Inst．13：208． 1943.
Symplocos persistens M．S．Huang \＆Y．F．Wu，Acta Phytotax．Sin．24：199． 1986.
Shrubs or trees，evergreen，to 15 m tall．Young branchlets brown－or ferrugineous－lanate to－ tomentose；mature branchlets brownish to dark purplish；pseudo－terminal vegetative buds $3-6 \mathrm{~mm}$ ， brown－to ferrugineous－sericeous．Petiole $4-11 \mathrm{~mm}$ ，not glandular；leaf blade oblong－ovate，ellip－ tic，oblong－elliptic，lanceolate，or oblong－lanceolate， $9.0-19.4 \times 2.2-7.0 \mathrm{~cm}, 2.5-4.5$ times as long as wide，subcoriaceous，typically drying abaxially grayish green，pale brown，or greenish brown and adaxially dark green to dark brown，abaxially tawny－to ferrugineous－lanate，adaxially lanate prox－ imally along midvein or glabrous，midvein adaxially impressed，secondary veins 5－14 on each side of midvein，base cuneate to rounded，margin serrate and planar or slightly revolute，apex long－ acuminate to occasionally caudate．Inflorescences spikes or glomerules， $0.5-2.0 \mathrm{~cm}, 7-15$－flow－ ered；rachis ferrugineous－pilose to－sericeous；bract broadly ovate to orbicular， $1-4 \times 0.7-3.5 \mathrm{~mm}$ ， caducous or occasionally persistent，apex obtuse to rounded．Bracts and bracteoles abaxially ferrug－ ineous－sericeous，margin entire，not glandular．Pedicel absent；bracteoles lanceolate，1．5－3 $\times$ $0.7-1.5 \mathrm{~mm}$ ，caducous or persistent，apex acuminate．Hypanthium pilose to sericeous，subtending articulation present．Calyx limb gamopetalous for ca． 0.3 mm ；lobes oblong，oblong－ovate，ovate， or broadly deltoid， $0.8-1.6 \times 0.7-1.2 \mathrm{~mm}$ ，sparsely to densely sericeous，margin ciliate and rarely glandular，apex obtuse to rounded．Corolla white to pale yellow， $2.5-4 \mathrm{~mm}$ ，membranous， gamopetalous only at base；lobes narrowly oblong to oblanceolate，glabrous，adaxially smooth． Stamens ca．35－50，adnate to corolla only at base，longest 4－6 mm； filaments not abruptly constricted apically，smooth．Disk cylindrical， white－to ferrugineous－lanate．Style 3－5．5 mm，glabrous．Fruit 7－10× $2.5-5 \mathrm{~mm}$ ，cylindrical，pilose；endocarp indurate throughout， 3 locules developed，perimeter ca．9－13－ribbed．Seeds straight．

Nooteboom（1975）placed this species under Symplocos macro－ phylla（as var．sulcata（Kurz）Nooteboom）but later Wu and Nooteboom（1996）and Nooteboom（2003）recognized it as distinct． Symplocos sulcata is clearly distinguishable from S．macrophylla by its glomerules or short spikes（versus elongate spikes or racemes）．Wu and Nooteboom（1996）and Nooteboom（2003）placed S．glandu－ losopunctata Y．F．Wu from Xizang Province，China as a synonym of S．sulcata，but in our opinion S．glandulosopunctata should be recog－ nized as distinct on the basis of its elongate racemes．It has not yet been collected in Gaoligong Shan but might be expected to occur there．

Symplocos sulcata is known in Gaoligong Shan only from the Baihualing area，where it is a common medium－size understory tree．

Selected Illustrations．－R．F．Wu，Fl．Reipubl．Popularis Sin．60（2）：50 t．19（1－6）， 65 t．23（14－18）．1987；G．H．Zhu，ed．Fl． China Ill．15：t．187（1－6），t．193（11－15）． 2000.

Phenology．－Fl．May－Nov，fr．Mar－Oct．
Distribution and habitat．－Subtropical broadleaved ever－ green forest and thickets； $1400-1500 \mathrm{~m}$ ．In GLGS：CHINA．Yunnan： Longyang Qu（Mangkuan Xiang）；Figure 22．Outside of GLGS： Yunnan，Xizang［Myanmar，Thailand］．

Local name．－滇灰木 dian hui mu


Figure 22．Distribution map of Symplocos sulcata in the GLGS region．

Additional specimens examined.- CHINA. YUNNAN: LONGYANG QU. Mangkuan Xiang. Yutang, Baihualing, E side of Gaoligong Shan, 1470 m, 6 Jul 2001, GLGS 14100 (CAS, KUN); Baihualing Cun, Zaotang area, E side of Gaoligong Shan, $1590 \mathrm{~m}, 9$ Sep 2003, GLGS 18964 (CAS, KUN); Baihualing, 1777 m, 2 Jun 2005, GLGS 25373 (CAS).

13. Symplocos sumuntia Buchanan-Hamilton ex D. Don, Prodr. Fl. Nepal. 145. 1825. Type.Nepal. Narainhetty, N. Buchanan-Hamilton s.n. (holotype: BM; isotype: K).

Symplocos caudata Wallich ex G. Don, Gen. Syst. 4:3. 1837.
Symplocos sumuntia var. floribunda A. de Candolle, Prodr. 8:255. 1844.
Symplocos botryantha Franchet, Nouv. Arch. Mus. Hist. Nat., ser. 2, 10:60. 1888.
S. botryantha var. stenophylla Brand, Repert. Spec. Nov. Regni Veg. 3:217. 1906.
S. cavaleriei H. Léveillé, Repert. Spec. Nov. Regni Veg. 9:77. 1910.

Symplocos punctata Brand, Repert. Spec. Nov. Regni Veg. 3:217. 1906.
Symplocos caudata var. macrantha Handel-Mazzetti, Beih. Bot. Centralbl. 62(B):18. 1943.
Shrubs to trees, evergreen, to 9 m tall. Young branchlets white- or brown-puberulent, occasionally also pilose, glabrescent; mature branchlets greenish to dark brownish; pseudo-terminal vegetative buds 2.5-4 mm, yellow- or pale ferrugineous-pilose-sericeous or rarely glabrous. Petiole 4-10 mm , usually with 1 or 2 pairs of glands, glands frequently caducous; leaf blade elliptic, narrowly elliptic, slightly obovate, or slightly oblanceolate, $4.8-9.7 \times 2.1-3.3 \mathrm{~cm}, 2.1-2.6(-3.6)$ times as long as wide, chartaceous, typically drying yellowish green, abaxially glabrous or occasionally sparsely long-strigose, adaxially minutely puberulent and occasionally also pilose proximally on midvein, midvein adaxially impressed, secondary veins 5-8 on each side of midvein, base cuneate, margin crenate-serrate and revolute, apex abruptly acuminate to caudate. Floral buds axillary or often pseu-do-terminal, conical to subglobose, $2-3 \mathrm{~mm}$; scales suborbicular to orbicular, glabrous or strigillose. Inflorescences pseudo-terminal or axillary, simple racemes, 1-4 cm, 2-18-flowered; rachis pale yellow villous; bract ovate to obovate, apex rounded to obtuse. Bracts and bracteoles caducous, keeled, yellow sericeous at least medially, margin ciliate to ciliolate and occasionally glandular. Pedicel $1-3 \mathrm{~mm}$; bracteoles elliptic, lanceolate, or narrowly deltoid, covering less than half of hypanthium, apex acuminate. Hypanthium glabrous, subtending articulation apical-medially. Calyx limb gamosepalous for $1-2 \mathrm{~mm}$; lobes triangular-ovate, margin usually ciliolate and not glandular, apex acute to obtuse. Corolla yellow, $4-5 \mathrm{~mm}$, membranous, gamopetalous only at base; lobes broadly elliptic, glabrous, adaxially smooth. Stamens ca. 25-35, adnate to corolla only at base, longest 5-7 mm; filaments not abruptly constricted apically, smooth. Disk annular, glabrous. Style $4.5-6.5 \mathrm{~mm}$, glabrous. Fruit ampulliform to ovoid, $7-8 \times \mathrm{ca} .5 \mathrm{~mm}$, glabrous; endocarp indurate throughout, 1 or 2 locules developed, perimeter smooth. Seeds curved, ramified.

This species is widespread southern and eastern China, but appears to be rare in Gaoligong Shan. The species can appear similar in leaf morphology to Symplocos viridissima, but the pubescent hypanthium and glabrous disk of $S$. viridissima serve to diagnostically distinguish it from $S$. sumuntia, at least in Gaoligong Shan.

Selected Illustrations.- R.F. Wu, Fl. Reipubl. Popularis Sin. 60(2):23 t. 6(1-13). 1987; G.H. Zhu, ed. Fl. China IIl. 15:t. 175(1-13). 2000.

Phenology. - Fl. Feb-Nov, fr. Apr-Nov.
Distribution and habitat.- Mixed forests, subtropical evergreen broadleaf forest; 1300-2500 m. In GLGS: CHINA. Yunnan: Lushui Xian (Liuku Zheng), Tengchong Xian (Dazuo Xiang. Guyong Xiang. Mingguang Xiang, Qushi Xiang, Zhonghe Xiang), Yingjiang Xian (Tongbiguan Xiang): Figure 23. Outside of GLGS: Fujian, Guangdong, Guangxi, Guizhou, Hainan, Hubei, Hunan. Jiangsu, Jiangxi. Sichuan, Taiwan, Yunnan, Zhejiang [Bhutan, India, Japan, Korea,

Malaysia, Myanmar, Nepal, Thailand, Vietnam].
Local name. - 山矾 shan fan.
Additional specimens examined.- CHINA. YUNNAN: LUSHUI XIAN. Liuku Zheng. Shweli Salween divide, $7000-8000 \mathrm{ft}$., Mar 1925, F 26236 (A, E, K). TENGCHONG XIAN. Dazuo Xiang. Hills to NE of Tengyueh, 6000-7000 ft., Jun 1912, F 8360 (A, E, K). Guyong Zheng. Hou Qiao, Hei Ni Tang, 1950 m, 19 May 1964, Wu 6692 (KUN). Mingguang Xiang. Shweli Salween divide, 7000-8000 ft., Apr 1931, F 29378 (E). Qushi Xiang. Shweli Valley, 7000-8000 ft., Mar 1931, F 29454 (E); Shweli River drainage basin and environs of Tengyueh, 1 Feb 1923, Rock 7987 (A). YINGJANG XIAN. Tongbiguan Xiang. $1350 \mathrm{~m}, 8$ Apr 1985, Fragrance Resources Expedition 85-118 (KUN); 1350 m, 8 Apr 1985, Fragrance Resources Expedition 85-149 (KUN).
14. Symplocos theifolia D. Don, Prodr. Fl. Nepal 145. 1825! Type.- Nepal. Narainhetty, 3 Nov 1802, F. Buchanan-Hamilton s.n. (holotype: BM!).

Symplocos phyllocalyx C.B. Clarke in J.D. Hooker, Fl. Brit. India. 3. 575. 1882.

Symplocos setchuensis Brand, Bot. Jahrb. Syst. 29:528. 1900. Dicalix setchuensis (Brand) Migo, Bull. Shanghai Sci. Inst. 13:205. 1943.
Symplocos henryi Brand in Engler, Pflanzenr. 6(IV. 242):67. 1901.
Symplocos multipes Brand, Repert. Spec. Nov. Regni Veg. 3:216. 1906.
Symplocos discolor Brand, Feddes Repert. Spec. Nov. Regni Veg. 3:216. 1906. Symplocos coronigera H. Léveillé, Repert. Spec. Nov. Regni Veg. 10:431. 1912.
Symplocos xanthoxantha H. Léveillé, Bull. Acad. Int. Geogr. Bot. 24:283. 1914.


Figure 23. Distribution map of Symplocos sumutia in the GLGS region.

Symplocos sinuata Brand, Repert. Spec. Nov. Regni Veg. 14:326. 1916.
Symplocos potaninii Gontscharow, Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 5:100. 1924.
Dicalix shinodanus Migo, Bull. Shanghai Sci. Inst. 13:205. 1943.
Shrubs or trees, evergreen, to 12 m tall. Young branchlets glabrous or rarely sparsely tomentellous, puberulent, or lanate, trichomes not incurved; mature branchlets greenish, often purplish mottled; pseudo-terminal vegetative buds $0.5-1.9 \mathrm{~cm}$, glabrous except for often ciliolate scale margins. Petiole $0.6-1.5 \mathrm{~cm}$, glabrous, not glandular; leaf blade elliptic to oblanceolate, $6.2-12.0 \times 1.9-3.8$ $\mathrm{cm}, 2.1-3.8$ times as long as wide, subcoriaceous, typically drying green to yellowish green, both surfaces glabrous, midvein adaxially prominent, secondary veins 7-14 on each side of midvein, base cuneate, margin serrulate and slightly revolute, apex acuminate. Inflorescences pseudo-terminal or axillary, simple or basally branched compact spikes, $0.6-2 \mathrm{~cm}, 1-10$-flowered (branches often 1 -flowered); rachis white-puberulent. Bracts and bracteoles, broadly ovate to suborbicular, isomorphic or bracts slightly larger, $0.7-2.0 \times 0.9-2.4 \mathrm{~mm}$, persistent, glabrous or rarely strigillose, margin entire or ciliolate but not glandular, apex acute to rounded. Pedicel absent; bracteoles covering less than half of hypanthium. Hypanthium glabrous, subtending articulation present. Calyx limb not gamosepalous; lobes $0.9-2.5 \times 0.9-2.3 \mathrm{~mm}$, semi-oblong, broadly ovate, or semi-orbicular, glabrous, margin entire or ciliolate, apex rounded. Corolla white, yellow, or green, $3.5-5 \mathrm{~mm}$, membranous, gamopetalous only at base; lobes oblong, slightly obovate, or linear-oblong, glabrous, adaxially smooth. Stamens $10-40$, adnate to corolla only at base, longest $4.5-6 \mathrm{~mm}$; filaments not abruptly constricted apically, smooth. Disk 5-lobed or low-annular, white-lanate. Style 2.5-6 mm,


Figure 24. Fruiting branch of Symplocos theifolia with galled fruit. Photo by M. Watson.
glabrous or occasionally strigose to hispidulous. Fruit blue. cylindrical to broadly elliptic, $8-15 \times$ 4-8 mm, glabrous: endocarp indurate throughout. 1 to 3 locules developed, perimeter smooth; galled fruit (as evident from persistent apical remains of unopened corolla and androecium) common, globose, $6-14 \times 4-10 \mathrm{~mm}$, endocarp thin or absent. Seeds U -shaped.

Symplocos theifolia is one of the most common species in the Gaoligong Shan. In the sterile condition it can still be easily distinguished from other species of Symplocos by the combination of the prominent leaf blade midvein adaxially and the glabrous pseudo-terminal buds. Most of the fruit of this species, at least in Gaoligong Shan. are sterile and apparently galled, whence they are slightly larger and swollen than fertile fruit. and without a well developed endocarp. In such cases the unopened corolla is often seen to remain attached to the fruit apex.

This species is recognized here in the broad sense, i.e., sensu Nooteboom $(1975,2005)$ and Wu and Nooteboom (1996) as opposed to the treatment of Wu (1987) in which seven species were recognized. Li et al. (2000) recognized the segregate Symplocos setchuensis in Gaoligong Shan. Wu (1987) distinguished this species from S. theifolia by the length and shape of the inflorescence, but we can detect no consistent differences in these features in correlation with any other characters throughout the distribution in Gaoligong Shan.

Nooteboom (1975) used the name Symplocos lucida (Thunberg) Siebold \& Zuccarini for this species but. based on the discussion in Nagamasu (1993), corrected it to S. theifolia [interactive computerized key and list of synonyms on CD-ROM cited in Nooteboom (2005)].

Selected Illestrations.- R.F. Wu. Fl. Reipubl. Popularis Sin. 60(2):11 t. 1(1-12), 12 t. 2(1-6), 14 t. 3(1-6). 1987; G.H. Zhu, ed. Fl. China Ill. 15:t. 170(1-12), t. 171(1-6), 172(1-6). 2000.

## Photographic image．－Figure 24.

Phenology．－Fl．Mar－Dec，Fr．May－Dec．
Distribution and habitat．－Coniferous forest，Deciduous broadleaf forest，Subtropical evergreen broadleaf forest，mixed Subtropical broadleaved evergreen forest and Coniferous forest； 1800－3400 m．In GLGS：CHINA．Xizang：Zayü Xian（Tsarong Xiang）．Yunnan：Fugong Xian（Lishadi Xiang，Lumadeng Xiang， Shangpa Zheng），Gongshan Xian（Bingzhongluo Xiang，Cikai Zheng，Dulongjiang Xiang），Lushui Xian（Luyobenzhuo Xiang）， Tengchong Xian（Guyong Zheng，Jietou Xiang，Puchuan Xiang， Qushi Xiang，Zhonghe Xiang），MYANMAR．Kachin．Myitkyina District（Chibyaw Township）；Figure 25．Outside of GLGS：Anhui， Fujian，Gansu，Guangdong，Guangxi，Guizhou，Hainan，Hubei， Hunan，Jiangsu，Jiangxi，Sichuan，Taiwan，Xizang，Yunnan，Zhejiang ［Bhutan，Cambodia，India，Indonesia，Japan，Laos，Malaysia， Myanmar，Thailand，Vietnam］．

LOCAL NAME．－光亮山矾 guang liang shan fan
Additional specimens examined．－CHINA．XIZANG：ZAYÜ
XIAN．Tsarong Xiang．Tsamputang Snow Range，Mount Kengyichunpo and region of Champutong，Salween－Irrawaddy watershed， 10000 ft ．，1923，Rock 10234 （A）．YUNNAN：F 11395 （K）；1917，F 17288 （A，K）； 2300 m， 1935－1936，Wang 88262 （KUN）；E slope of GLGS， 2920 m， 4 May 1950，Wu 9040 （KUN）．FUGONG XIAN．Sha La He Luo，Bijiang， 3000 m， 16 Jul 1978，QX 1178 （KUN）．Lishadi Xiang．Moist canyon just S of the Shibali Logging Station on the rd from the Nujiang to Yaping Pass，E side of Gaoligong Shan， 2506 m， 28 Apr 2004，GLGS 19996 （CAS）；vicinity of Shibali Logging Station on the rd from the Nujiang to Yaping Pass，E side of


Figure 25．Distribution map of Symplocos theifolia in the GLGS region． Gaoligong Shan， 2485 m， 28 Apr 2004，GLGS 20042 （CAS）；between Shibali Logging Station and Yaping Pass，ca． 4 km W of Shibali，from the Nujiang to Yaping Pass，E side of Gaoligong Shan， 2821 m， 2 May 2004，GLGS 20080 （CAS）；between Shibali Logging Station and Yaping Pass，ca． 7.2 km W of Shibali，from the Nujiang to Yaping Pass，E side of Gaoligong Shan， $2999 \mathrm{~m}, 2$ May 2004，GLGS 20188 （CAS）；between the Shibali Logging Station and Yaping Pass，ca． 8.5 km W of Shibali，from the Nujiang to Yaping Pass，E side of Gaoligong Shan， 3106 m， 8 May 2004，GLGS 20460 （CAS）；between the Shibali Logging Station and Yaping Pass，near Km 18 on the rd from the Nujiang to Yaping Pass，E side of Gaoligong Shan， 3030 m， 1 May 2004，GLGS 20878 （CAS）；Yaduo Cun，above Shibali along the N side of S fork of Yamu He，E side of Gaoligong Shan， 2900 m， 15 Aug 2005，GLGS 28310 （CAS）．Lumadeng Xiang．Yaping Cun， below Amero Pass along the rd back down to the confluence of the N and S fork of Yamu He，E side of Gaoligong Shan， 2950 m， 13 Aug 2005，GLGS 27193 （CAS）； $2600 \mathrm{~m}, 28$ May 1982，QX 6981 （KUN）． Shangpa Zheng． $2600 \mathrm{~m}, 16$ Sep 1933，Tsai 54255 （A，KUN）； $2800 \mathrm{~m}, 10$ Oct 1934，Tsai 58706 （A，KUN）； $2800 \mathrm{~m}, 20$ Oct 1934，Tsai 58843 （A，KUN）．GONGSHAN XIAN．Pan Shan Te to Yi Bi Di， $2800 \mathrm{~m}, 3$ May 1960，NW Yunnan Expedition 10034 （KUN）；the first district，A Lu La Ka，Long Po， 2920 m， 1 Jun 1960，Wu 9241 （KUN）；the ninth district，Pang Sha Wu to Yi Bi Di， 2800 m， 30 May 1960，Wu 10013 （KUN）． Bingzhongluo Xiang．Middle part of Bingzhongluo River，2500－3400 m， 30 Aug 1979，X．F．Deng 791352 （KUN）；Chang Pu Tong， 3300 m， 20 Sep 1940，Feng 7911 （KUN，PE）；Ni Wa Qing Long A Bao Di， 2200 m， 13 Oct 1956，P．I．Mao 560 （KUN）；Champu tung，Bar－ru－Lah，Salween－Chukiang divide， $2300 \mathrm{~m}, 1$ Oct 1935， Wang 67551 （A，KUN，PE）．Cikai Zheng．Hei Pu Shan， 13 Oct 1940，Feng 8407 （KUN）；E side of Gaoligong Shan，along the Danzhu He on the rd from Nu Jiang at Danzhu to the Myanmar border， $2650 \mathrm{~m}, 1 \mathrm{Jul}$ 2000， GLGS 11829 （CAS，GH，KUN）；Danzhu，E side of Gaoligong Shan，around the border between Myanmar and China near Danzhuyakou， 3378 m， 14 Apr 2002，GLGS 14234 （CAS，KUN）；E side of Gaoligong Shan，W of Gongshan，along the Pula He on the trail around No． 12 Bridge， 2770 m， 2 May 2002，GLGS 14847 （CAS，

KUN); E side of Gaoligong Shan, W of Gongshan, along the Pula He on the trail around No. 12 Bridge, 2770 m, 2 May 2002, GLGS 14849 (CAS, KUN); E side of Gaoligong Shan, W of Gongshan, along the Pula He on the trail from Qiqi to No. 12 Bridge and Dulongjiang Valley, $2500 \mathrm{~m}, 3$ May 2002, GLGS 14874 (KUN); along rd from Gongshan to Kongdang, E side of Gaoligong Shan, 2800 m, 23 Sep 2002, GLGS 16513 (CAS, KUN); Labadi, along the rd from Gongshan to Kongdang, E side of Gaoligong Shan, 2970 m, 30 Sep 2002, GLGS 16788 (CAS, KUN); along rd from Gongshan to Kongdang, on the E side of Gaoligong Shan above the Pula He, 3100 m, 3 Oct 2002, GLGS 16902 (CAS, KUN [2]); E side of Gaoligong Shan at Km 34 on the rd from Gongshan to Kongdang, 2890 m, 13 Nov 2004, GLGS 22611 (CAS). Dulongjiang Xiang. Kongdang, on the E side of the Dulong Jiang, $2600 \mathrm{~m}, 2$ Jan 1991, GLGS 1587 (CAS, KUN); Qiawudang, S side of the Gamolai He, ca. 4 km SE of Bapo on the E side the Dulong Jiang, $2650 \mathrm{~m}, 25$ Mar 1991, GLGS 4990 (CAS, KUN [2]); Dizhengdang, on the W side of the Dulong Jiang, $1880 \mathrm{~m}, 14$ Apr 1991, GLGS 5737 (CAS); Sandui, NE of Shigong Bridge and NW of Xishaofang on the trail from Gongshan to Bapo, $2500 \mathrm{~m}, 20$ May 1991, GLGS 6925 (KUN); Da Ba Yi, $2500 \mathrm{~m}, 6$ Sep 1956, P. I. Mao 429 (KUN); Dulongjiang to Dongshaofang, 2600 m , 22 Jul 1982, QX 8395 (KUN); Dulongjiang to Dongshaofang, 2200-2400 m, 26 Jul 1982, QX 8604 (KUN); 2300 m, 30 Aug 1982, QX 9764 (KUN); Taron Taru divide, Bucashwang Valley, $2000 \mathrm{~m}, 3$ Sep 1937, Yü 20119 (KUN); Taron Taru divide, Bucashwang Valley, 2600 m, 5 Nov 1937, Yï 20972 (A, A, KUN); SalweenKiukiang divide, Swangchiang, 2800 m, 15 Jul 1938, Yü 22104 (A, E, KUN); Salween-Kiukiang divide, Swangchiang, 2650 m, 11 Nov 1938, Yü 22960 (A, KUN, PE); Salween-Kiujiang divide, Si Wang Qiang, 2650 m, 4 Nov 1938, Yü 22961 (KUN). LUSHUI XIAN. Luobenzhuo Xiang. E'ga Cun, on forest rd at Km 30, E side of Gaoligong Shan, $2800 \mathrm{~m}, 8$ Aug 2005, GLGS 25797 (CAS). TENGCHONG XIAN. Mountain near Tengyueh, $3300 \mathrm{~m}, 29$ Sep 1974, C.K. Schneider 2732 (W). Guyong Zheng. Dan Za, $2100 \mathrm{~m}, 17$ Oct 1983, Q. Lin 770683 (KUN). Jietou Xiang. Shweli-Salween divide, 9000-10000 ft., Nov 1924, F 25359 (E, K, W); N of Datang, $1850 \mathrm{~m}, 27$ Oct 1998, GLGS 11021 (CAS, KUN); E of Datang, on the W slope of Gaoligong Shan, 2180 m, 30 Oct 1998, GLGS 11260 (KUN); Datang Cun, E of Datang on the W slope of Gaoligong Shan, 2180 m, 30 Oct 1998, GLGS 11269 (CAS, GH, KUN). Mazhan Xiang. Ma-Chang-Kai Valley, N of Tengyueh, 6000 ft., Feb 1913, F 9533 (E). Puchuan Xiang. Laoqing Forest Station, 1880-3120 m, W.C. Yin 60-1340 (KUN). Qushi Xiang. Daba, 2100 m, 18 May 1997, Z.L. Dao et al 9481 (KUN [2]); W flank of the ShweliSalween divide, $9000-10000 \mathrm{ft}$., Aug 1912, $F 9038$ (BM, E, K); hills NE of Tengyueh, 7000 ft ., Nov 1912, F 9330 (K, E, W); Shweli-Salween divide, 7000 ft., Aug 1913, F 12016 (A, BM, E, K); Shweli River drainage basin to summit of Shweli-Salween watershed E of Tengyueh, 1 Nov 1922, Rock 7608 (A); Shweli River drainage basin to summit of Shweli-Salween watershed E of Tengyueh, 8000 ft ., 1 Nov 1922, Rock 7633 (A). Zhonghe Xiang. Flank of volcanic mountain NW of Tengyueh, 7000-8000 ft., Jun 1912, F 8064 (E, W). MYANMAR. Between Sadon and the Yunnan Chinese border at Changtifang and Kambaiti, 1 Nov 1922, Rock 7393 (A, W). KACHIN: MYITKYINA DISTRICT. Chibyaw Township. Eastern flank of Sungku divide, 9000 ft ., May 1917, F 13786 (A, E, K).
15. Symplocos viridissima Brand in Engler, Pflanzenr. 6(IV. 242):41. 1901. TyPe.— India. Assam: W. Griffith 3659 (holotype: B, destroyed; isotype: GH, K, LE, W).

Symplocos araioura Merrill, Brittonia 4:164. 1941.
Symplocos ascidiformis Y.F. Wu, Acta Phytotax. Sin. 20:92. 1982.
Shrubs or trees, evergreen, to 3.5 m tall. Young branchlets glabrous or sparsely to rarely densely white- (rarely ferrugineous-) strigose to -hispidulous and sometimes also -puberulent; mature branchlets greenish or less commonly brownish; pseudo-terminal vegetative buds $2.5-6 \mathrm{~mm}$, sericeous. Petiole 2-6 mm; leaf blade elliptic, lanceolate-elliptic, or oblanceolate-elliptic, 4.5-12.7 $\times 1.3-3.8 \mathrm{~cm}, 2.7-4.1$ times as long as wide, chartaceous, typically abaxially drying pale green to pale grayish green and adaxially green to grayish green, abaxially sparsely tawny- to dull ferrugi-neous-strigose at least proximally along midvein, adaxially glabrous, midvein adaxially impressed, secondary veins $3-5(-7)$ on each side of midvein, base subrounded, cuneate, or slightly attenuate, margin serrulate, denticulate or rarely minutely and irregularly undulate and planar, apex caudate.

Inflorescences simple or branched racemes， $0.8-1.5 \mathrm{~cm}, 1-8$－flowered；rachis tawny－to pale brown－strigose．Bracts and bracteoles deltoid to ovate，$\pm$ isomorphic but bracts somewhat larger， $0.6-2.1 \times 0.4-0.9 \mathrm{~mm}$ ，caducous，strigillose，margin ciliate and often glandular，apex acute．Pedicel $1-4 \mathrm{~mm}$ ；bracteoles covering less than half of hypanthium．Hypanthium strigillose，subtending articulation present．Calyx limb not gamosepalous；lobes deltoid－ovate to hemispherical，0．8－1．2× $1.0-1.5 \mathrm{~mm}$ ，strigillose，margin ciliolate and not glandular，apex broadly acute to rounded．Corolla white，3－4 mm，membranous，gamopetalous only at base；lobes oblong，ovate－elliptic，linear－ oblong，or oblanceolate，glabrous，adaxially smooth．Stamens ca．35－45，adnate to corolla only at base，longest 4－6 mm；filaments not abruptly constricted apically，smooth．Disk low annular， glabrous．Style 4－5 mm，glabrous．Fruit blue，narrowly ampulliform to rarely subglobose at matu－ rity，（6－）7－10 $\times 4-5 \mathrm{~mm}$ ，sparsely strigillose；endocarp indurate throughout， 1 locule developed，perimeter smooth or shallowly ca．11－ ribbed．Seeds curved．

Li et al．（2000）list two specimens（Feng 24206 and $Q X$ Expedition 82－8834）under the nomen nudum＂Symplocos caudi－ formis Huang ex C．Chen \＆Gao＂that clearly fall within the range of morphological variation of S．viridissima．

See also comments under Symplocos sumuntia．
Selected Illustrations．－R．F．Wu，Fl．Reipubl．Popularis Sin．60（2）：31 t．10（5－7）， 46 t．17（1－4）．1987；G．H．Zhu，ed．Fl．China Ill．15：t．180（5－7），t．184（1－4）． 2000.

Phenology．－Fl．Mar－May，fr．Jun－Sep．
Distribution and habitat．－Subtropical broadleaved ever－ green forest and thickets； $1200-2200 \mathrm{~m}$ ．In GLGS：CHINA．Yunnan： Gongshan Xian（Bingzhongluo Xiang，Dulongjiang Xiang）；Figure 26．Outside of GLGS：Guangdong，Guangxi，Guizhou，Hainan， Xizang，S Yunnan［NE India，Myanmar，Vietnam］．

Local name．－绿枝山矾 lu zhi shan fan
Additional specimens examined．－CHINA．YUNNAN： GONGSHAN XIAN．W slope of Gaoligong Shan， $2400 \mathrm{~m}, 28$ Jul 1982，QX 8834 （KUN［2］）．Bingzhongluo Xiang．Sichun，Miliwaluo， 1200 m， 12 Apr 1959，Feng 24406 （KUN）．Dulongjiang Xiang． 1350 m， 15 Nov 1959，Feng 24148 （KUN［2］）；Miliwage，E bank of Dulongiang， 1200 m， 12 Nov 1959， Feng 24206 （KUN）；Ji Mu Deng， 1200 m， 19 Nov 1990，GLGS 539 （KUN）； Nei Ben La， 1300 m， 19 Nov 1990，GLGS 557 （KUN）；the third team， 1800 m， 22 Nov 1990，GLGS 788 （KUN）；Ji Mu Deng， 1400 m， 6 Dec 1990，GLGS 854 （KUN［2］）；Ga Mo Lai He， 1350 m， 30 Dec 1990，GLGS 1458 （KUN）；


Figure 26．Distribution map of Symplocos viridissima in the GLGS region． Ga Mo Lai He， 1400 m， 25 Jan 1991，GLGS 2387 （KUN）；Mei Li Wang， 2300 m， 16 Jan 1991，GLGS 3058 （KUN）；Mei Li Wang， 2100 m， 16 Jan 1991，GLGS 3068 （KUN）；Ga Mo Lai He， 1350 m， 26 Jan 1991，GLGS 3409 （KUN）；Nei Pu La， 1300 m， 6 Feb 1991，GLGS 3950 （KUN）；vicinity of Nengpula on the W side of the Dulong Jiang just W of Hongxin Qiao（Red Star Bridge）ca． 0.5 km SW of Bapo， $1330 \mathrm{~m}, 29$ Oct 2004，GLGS 20783 （CAS）；between Shigong Qiao and Panjiasheng on trail from Bapo to Gongshan via Qiqi on the W side of Gaoligong Shan，2100－2200 m， 30 Oct 2004，GLGS 22000 （CAS）；W slope of Gaoligong Shan， 2400 m ， 28 Jul 1982，QX 8834 （KUN）．

16．Symplocos xylopyrena C．Y．Wu ex Y．F．Wu，Acta Phytotax．Sin．20：91．1982．Symplocos ramosissima Wallich ex G．Don var．xylopyrena（C．Y．Wu ex Y．F．Wu）Nooteboom，Blumea 50：409． 2005．Type．－China．Xizang：Mêdog Xian， 2000 m， 12 August 1974，Qinghai－Xizang Expedition 74－1814（holotype：PE；isotype：KUN！）．

Shrubs or trees，evergreen，to 6 m tall．Young branchlets glabrous or proximally sparsely white－ ，tawny－，or yellow－puberulent；mature branchlets dark purplish；pseudo－terminal vegetative buds $8-11 \mathrm{~mm}$ ，glabrous except for ciliolate scale margins．Petiole $3-8 \mathrm{~mm}$ ，not glandular；leaf blade nar－ rowly elliptic to slightly oblanceolate， $7.6-11.0 \times 2.9-3.8 \mathrm{~cm}, 2.6-3.9$ times as long as wide，mem－ branous to thinly chartaceous，drying green to greenish brown，abaxially glabrous，adaxially minutely white－hispidulous at least proximally along midvein otherwise glabrous，midvein adaxi－ ally impressed，secondary veins $13-17$ on each side of midvein，base broadly cuneate，margin entire and planar，apex acuminate．Inflorescences simple or branched racemes， $1-1.5 \mathrm{~cm}, 1-14$－flowered； rachis white－，ferrugineous－，or brown－puberulent．Bracts and bracteoles ovate to linear－deltoid，$\pm$ isomorphic but bracts somewhat larger， $1.2-1.8 \times 0.5-1 \mathrm{~mm}$ ，caducous，glabrous or sparsely puberulent apical－medially，margin ciliolate and not glandular，apex acute to acuminate．Pedicel 1－3 mm ；bracteoles covering less than half of hypanthium．Hypanthium glabrous，subtending articula－ tion present．Calyx limb not gamosepalous；lobes hemispherical to broadly deltoid，1－1．4×1－1．5 mm ，glabrous，margin ciliolate and not glandular，apex obtuse to rounded．Corolla white，ca． 6 mm ， membranous，gamopetalous only at base；lobes glabrous，adaxially smooth．Stamens ca．110，adnate to corolla only at base；filaments not abruptly constricted apically，smooth．Fruit ellipsoid to obovoid， $2.4-2.9 \times$ ca． 1.2 cm ，glabrous；endocarp with indurate part irregularly intercalated with network of softer spongy tissue， 2 locules developed，perimeter slightly irregularly undulate．Seeds straight．

Nooteboom（2005）has treated this species as a variety of Symplocos ramosissima．There are many morphological features，however，that distinguish S．xylopyrena from S．ramosissima such that the recognition of S．xylopyrena at the species level is justified （e．g．，pseudo－terminal vegetative buds $8-11 \mathrm{~mm}$ long and glabrous except for ciliate margins［versus $4-8 \mathrm{~mm}$ long and pubescent］；sec－ ondary leaf veins 13－17［versus 6－10］；bracteoles caducous［versus usually persistent］；hypanthium glabrous［versus strigillose or rarely glabrous］；calyx lobes $1-1.4 \mathrm{~mm}$［versus $0.6-1 \mathrm{~mm}$ ］；fruit 2．4－2．9× ca． 1.2 cm ［versus $0.7-1.1 \times 0.4-0.6 \mathrm{~cm}$ ］；and endocarp with a net－ work of soft spongy tissue［versus indurate throughout］）．

Selected Illustrations．－R．F．Wu，Fl．Reipubl．Popularis Sin．60（2）：40 t．15（1－8）；G．H．Zhu，ed．Fl．China Ill．15：t．185（1－8）． 2000.

Phenology．－Fl．May－Aug，fr．Aug－Dec．
Distribution and habitat．－Subtropical broadleaved ever－ green forests；1300－2200 m．In GLGS：CHINA．Yunnan：Gongshan Xian（Dulongjiang Xiang）；Figure 27．Outside of GLGS：Xizang， Yunnan．

## Local name．一 木核山矾 mu he shan fan

Additional specimens examined．－CHINA．YUNNAN： GONGSHAN XIAN．Dulongjiang Xiang．Nengpula，directly opposite Bapo on the W side of the Dulong Jiang， $1300 \mathrm{~m}, 21$ Nov 1990，GLGS 627 （CAS，KUN）；Mengdang，ca． 1.5 km S of Bapo on the E side of the Dulong Jiang， 1310 m， 14 May 1991，GLGS 6720 （CAS，KUN）；W side of Gaoligong Shan，W of Gongshan，on the trail from Qiqi to Bapo in the Dulong Jiang Valley，2050－2150 m， 17 Jul 2000，GLGS 12916 （CAS）；between Shigong Qiao and Panjiasheng on trail from Bapo to Gongshan via Qiqi on the W side of Gaoligong Shan．2100－2200 m． 30 Oct 2004，GLGS 21999 （CAS）； 2400 m， 28 Jul 1982，QX 8822 （KUN）；Bapo to Maku， 2400 m， 6 Aug 1982，QX


Figlre 27．Distribution map of Symplocos xylopyrena in the GLGS region．

8940 (KUN); Taron-Taru divide. Lahpi, 2000 m, 26 Aug 1938, Yüi 19946 (A); Tarou-Taru divide. Tangtehwang, 1600 m, 26 Aug 1938, Yüi 20862 (A).

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## Literature Cited

Angiosperm Phylogeny Group. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Botanical Journal of the Linnean Society 141:399-436.
Brand, A. 1901. Symplocaceae. Pages 205-274 in A. Engler, ed., Das Pflanzenreich IV. 242 (Heft 6). Engelmann, Leipzig, Germany.
Chaplin, G. 2006. Physical geography of the Gaoligong Shan area of southwest China in relation to biodiversity. Proceedings of the California Academy of Sciences 56:527-556.
Chen, H.S., H.G. Ye, and F.Y. Zeng. 2003. A new species of Symplocos (Symplocaceae) from China. Journal of Tropical and Subtropical Botany 11:169-170.
Fritsch, P.W., B.C. Cruz, F. Almeda, Y. Wang, and S. Shi. 2006. Phylogeny of Symplocos based on DNA sequences of the chloroplast trnC-trnD intergenic region. Systematic Botany 31:181-192.
Fritsch, P.W., and F. Almeda. In press. Revised infrageneric classification of Symplocos (Symplocaceae) based on phylogenetic data from DNA sequences and morphology. Taxon.
Greuter, W., ed. 1999. International Code of Botanical Nomenclature (Saint Louis code). Koeltz Scientific, Königstein, Germany.
Harris, J. G., and M. W. Harris. 2001. Plant Identification Terminology. An Illustrated Glossary, $2^{\text {nd }}$ ed. Spring Lake Publishing, Spring Lake, Utah, USA.
Kress, J.K., R.A. DeFillipps, E. Farr, and D.Y.Y. Kyi. 2003. A checklist of the trees, shrubs, herbs, and climbers of Myanmar. Contributions from the United States National Herbarium 45:1-590.
Li , H., H.J. Guo, and Z.L. Dao. 2000. Flora of Gaoligong Mountain. Science Press, Beijing, China.
Liu, A.-Z., and W.J. Kress. 2005. The Gaoligong Mountains of Southwest China and Northeast Myanmar. Pp. 86-92 in G.A. Krupnick and W.J. Kress, eds., Plant Conservation. A Natural History Approach. University of Chicago Press, Chicago, Illinois, USA.
Nagamasu, H. 1993. The Symplocaceae of Japan. Contributions from the Biological Laboratory of Kyoto University 28:173-260.
Nooteboom, H.P. 1975. Revision of the Symplocaceae of the Old World, New Caledonia Excepted. Universitaire Pers Leiden (Leiden Botanical Series, vol. 1).
Nooteboom, H.P. 1977. Symplocaceae. Pages 205-274 in C.G.G.J. van Steenis, ed., Flora Malesiana, series 1, vol. 8, part 2. Sijthoff \& Noordhoff, Alphen aan den Rijn, Netherlands.
Nooteboom, H.P. 1980. Review of Symplocos (Symplocaceae) from New Caledonia. Blumea 26:411-415.
Nooteboom, H.P. 1996. How to deal with complex species with two examples from east Asian Symplocos. Pages 335-340 in A. Zhang and S. Wu, eds., Floristic Characteristics and Diversity of East Asian Plants. China Higher Education Press, Beijing, China and Springer-Verlag, Berlin, Germany.
Nooteboom, H.P. 2005. Additions to Symplocaceae of the Old World including New Caledonia. Blumea 50:407-411.
Schónenberger, J., A.A. Anderberg, and K.J. Sytsma. 2005. Molecular phylogenetics and patterns of floral evolution in the Ericales. International Journal of Plant Sciences 166:265-288.

Stotz, D.F., E.J. Harris, D.K. Moskovits, K. Hao, S. Yi, and G.W. Adelmann, eds. 2003. China: Yunnan, Southern Gaoligongshan. Rapid Biological Inventories Report no. 4. The Field Museum, Chicago, Illinois, USA.
Thunberg, C.P. 1794-1805. Icones Plantarum Japonicarum. J.F. Edman, Uppsala, Sweden.
Wang, Y., P.W. Fritsch, S. Shi, F. Almeda, B.C. Cruz, and L.M. Kelly. 2004. Phylogeny and infrageneric classification of Symplocos (Symplocaceae) inferred from DNA sequence data. American Journal of Botany. 91:1901-1914.
Wu, R.F. 1987. Symplocaceae. Pages 1-77 in Z.Y. Wu, ed., Flora Reipublicae Popularis Sinicae vol. 60(2). Science Press, Beijing, China.
Wu, R.F., AND H.P. Nooteboom. 1996. Symplocaceae. Pages $235-252$ in Z.Y. Wu and P.H. Raven, eds., Flora of China: Myrsinaceae through Loganiaceae, vol. 15. Science Press, Beijing, China and Missouri Botanical Garden Press, St. Louis, Missouri, USA.
Ye, H.G., F.W. Xing, F.G. Wang, and F.Y. Zeng. 2003. A new species and a new synonym of Symplocos (Symplocaceae) from China. Journal of Tropical and Subtropical Botany 11:277-279.

## Apppendix 1

## Abbreviations for Collectors and Expeditions that Record Ten or More Symplocos Collections in the GLGS Area

| Abbreviation form | Original form |
| :--- | :--- |
| F | Forrest, George |
| Feng | Feng, K.M. |
| GLGS | (including 11 collecting activities with the same series of |
|  | numbers) |
|  | Dulong Jiang Investigation Team; |
|  | Gaoligong Shan Expedition; |
|  | Gaoligong Shan Biodiversity Survey: Li Heng, Bruce |
|  | Bartholomew, \& Dao Zhiling; Li Heng, Bruce Bartholomew, |
|  | Philip Thomas, Peter Fritsch, Dao Zhiling, Wang Zhonglan |
|  | \& Li Rong; Li Heng, Dao Zhiling \& Yin Liwei; Li Heng, |
|  | Dao Zhiling \& Yin Liwei; Li Heng, Dao Zhiling, Long |
|  | Chunlin, Li Rong \& Liu Yitao; Li Heng et al.; Li Heng, |
|  | Guo Huijin, Li Zhengbo \& Shi Xiaochun; Li Heng, Ji |
|  | Yunheng \& Li Rong |
|  | Qinghai-Xizang Expedition |
| QX | Rock, Joseph F. Charles |
| Rock | Tsai, H.T. |
| Tsai | Wang, C.W. |
| Wang | Wu, S.K. |
| Wu | Yü, T.T. |

## Appendix 2

## List of Species

1. Symplocos anomala Brand
2. Symplocos cochinchinensis (Loureiro) S. Moore
3. Symplocos dryophila C.B. Clarke
4. Symplocos glauca (Thunberg) Koidzumi
5. Symplocos glomerata King ex C.B. Clarke
6. Symplocos laurina (Retzius) Wallich ex G. Don
7. Symplocos oxyphylla Wallich ex A. de Candolle
8. Symplocos paniculata (Thunberg) Miquel
9. Symplocos pendula Wight
10. Symplocos racemosa Roxburgh
11. Symplocos ramosissima Wallich ex G. Don
12. Symplocos sulcata Kurz
13. Symplocos sumuntia Buchanan-Hamilton ex D. Don
14. Symplocos theifolia D. Don
15. Symplocos viridissima Brand
16. Symplocos xylopyrena C.Y. Wu ex Y.F. Wu

## Appendix 3

## Index to Exsiccatae

All specimens examined by the authors are listed alphabetically by collector, followed by collection numbers (and herbarium if anonymous). Numbers in parentheses correspond to those in the numerical list of species.
I.A. Abbay: 16 (3).

Bijiang Expedition: 609 (3); 972 (3); 1187 (3); 1350 (3); 1761 (3); 1945 (3).
J. Chen: 239 (8); 684 (8); 735 (11).
Z.L. Dao et al: 9465 (3); 9473 (11); 9478 (8); 9481 (14).
X.F. Deng: 791352 (14).

F: 1037 (6); 1095 (6); 6797 (8); 7457 (8); 7883 (8); 8056 (6); 8064 (14); 8147 (3); 8241 (3); 8360 (13); 8991 (3); 9038 (14); 9330 (14); 9533 (14); 9842 (8); 11395 (14); 11909 (3); 12016 (14); 12056 (3); 12093 (3); 12301 (5); 12748 (8); 13654 (3); 13786 (14); 13880 (8); 13884 (8); 15027 (8); 15653 (3); 15654 (3); 15668 (3); 15713 (5); 15716 (11); 15739 (11); 15771 (3); 15814 (3); 15842 (6); 15844 (6); 15904 (11); 16007 (3); 16067 (3); 16083 (11); 17288 (14); 17491 (6); 17522 (6); 17606 (11); 17627 (3); 17628 (5); 17629 (11); 17655 (5); 17717 (3); 17741 (6); 17745 (6); 17780 (3); 17889 (11); 18031 (11); 18234 (10); 18297 (5); 18311 (3); 18480 (6); 21620 (3); 21798 (11); 24007 (5); 24013 (5); 24018 (3); 24023 (8); 24082 (5); 24180 (11); 24372 (11); 24401 (6); 24402 (11); 24589 (11); 24641 (4); 24678 (11); 24704 (6); 25073 (9); 25159 (11); 25189 (6): 25241 (4); 25359 (14); 25653 (11); 25665 (8); 25758 (9); 25889 (8); 26236 (13); 26241 (5); 26335 (3); 26377 (3); 26467 (3); 26574 (5); 26635 (3); 26842 (11); 27104 (11); 27202 (3); 27211 (3); 27307 (11); 27411 (3); 27436 (6); 29378 (13); 29454 (13); 29837 (3).
R.J. Farrer: 1564 (3); 1621 (3).

Feng: 7497 (5); 7911 (14); 8407 (14); 24148 (15); 24206 (15); 24211 (9); 24336 (3); 24406 (15); 24425 (3); 24567 (3); 54558 (3).
Fragrance Resources Expedition: 125 (8); 145 (8); 210 (8); 277 (8); 85118 (13); 85149 (13).
GLGS: 89 (3): 539 (15); 557 (15); 627 (16); 742 (3); 785 (3): 788 (15); 854 (15); 985 (5); 1095 (3); 1107 (3); 1393 (3); 1458 (15); 1504 (5); 1539 (5); 1554 (6); 1587 (14): 1758 (6); 1935 (5); 1943 (3); 1943 (6); 1949 (5); 1958 (6); 1994 (5); 2125 (5): 2144 (5): 2387 (15); 3056 (3); 3058 (15); 3061 (5); 3066 (3); 3068 (15); 3145 (3); 3167 (3): 3202 (6): 3204 (5): 3336 (6): 3409 (15): 3680 (5); 3845 (5); 3896 (5); 3950 (15); 4288 (5); $4290(3) ; 4321(5) ; 4329(5) ; 4332$ (6); $4345(6) ; 4579(3) ; 4584(3) ; 4600(3) ; 4635(5) ; 4662(5) ; 4779$ (3); 4780 (3); 4781 (3); 4859 (11); 4865 (3); 4900 (5); 4941 (3); 4968 (3); 4990 (14); 5077 (5); 5203 (3); 5204 (3): 5205 (11); 5229 (3); 5235 (5); 5236 (3); 5257 (3); 5278 (5); 5357 (3); 5405 (3); 5467 (3); 5500 (3); 5703 (3); 5737 (14); 5919 (3); 6074 (3); 6111 (3); 6163 (5); 6293 (3); 6595 (5); 6658 (9); 6666 (5); 6720 (16): 6801 (5); 6802 (5): 6819 (5); 6840 (3); 6898 (11): 6911 (5): 6925 (14); 7024 (3); 7038 (3); 7049 (3); 7524 (5); 7590 (11); 7705 (5); 9309 (5); 9340 (11); 9387 (5); 9407 (11); 9509 (3); 9531 (3); 9778 (1); 10059 (3): 10888 (8): 11021 (14): 11260 (14); 11269 (14): 11369 (8); 11570B (6); 11829 (14); 11843 (3); 11972 (5); 11976 (5); 12255 (5); 12300 (3): 12307 (3): 12507 (3); 12916 (16); 12917 (5); 12949 (3); 13072 (11); 13161 (11); 13202 (6); 13283 (6); 13648 (11); 13886 (5); 14100 (12); 14135 (3); 14234 (14); 14444 (3); 14461 (3); 14473 (3): 14474 (3): 14669 (3): 14672 (5); 14689 (3); 14771 (5); 14775 (5); 14847 (14); 14849 (14): 14864 (5): 14874 (3): 14874 (14): 15208 (3): 16513 (14); 16521 (3); 16788 (14); 16902 (14); 17103 (3): 17271 (5): 17319 (11): 17558 (11): 17593 (6): 17725 (11): 17896 (11); 17937 (8); 17968 (6); 17971 (11): 17978 (6); 17984 (6); 18030 (6): 18365 (11); 18473 (11); 18520 (6); 18525 (6); 18577 (5); 18666 (6); 18694 (11); 18759 (5); 18780 (11): 18848A (11); 18964 (12); 19993 (3); 19996 (14); 20042 (14); 20080 (14): 20090 (3): 20150 (3): 20188 (14); 20241 (5); 20292 (3); 20368 (5); 20383 (3); 20460 (14); 20783 (15): 20878 (14); 21981 (3); 21999 (16): 22000 (15): 22611 (14); 22625 (5); 23052 (3); 23307 (3); 23726 (11): 23755 (11): 23759 (11): 23803 (11): 23808 (11): 23917 (10); 23935 (3); 24111 (5); 24299 (5): 24535 (3): 24616 (11): 24641 (11): 24734 (6): 24756 (6): 24929 (11); 25064 (5); 25070 (6); 25119 (11); 25162 (5): 25179 (11): 25212 (11): 25338 (11); 25373 (12); 25797 (14); 26053 (11); 26061 (11); 26543 (3); 26909 (3): 26910 (3): 26913 (3): 26918 (3); 27168 (3); 27193 (14): 27228 (3); 27278 (3); 27280 (3); 28310
(14); 28431 (3); 28432 (3); 28470 (3); 28486 (3); 28487 (3); 28824 (11).
H.F. v. Handel-Mazzetti: 9461 (5); 9604 (11).
W.D. Kermode: 16694 (3); 17208 (3); 17282 (3).
F. Kingdon Ward: 16 (3).

Mg Kyaw: 50 (7).
Q. Lin: 770683 (14).
F. Ludlow: 13033 (8).
P. I. Mao: 429 (14); 560 (14).

Naw Mu Pa: 15505 (5).
Nujiang Expedition: 71 (3); 445 (5); 1814 (11); 7040 (11); 791252 (5); 7968 (5).
NW Yunnan expedition: 10034 (14).
R. C. Ching: 50247 (5).

QX: 1178 (14); 6981 (14); 7018 (3); 7079 (5); 7095 (5); 7456 (3); 7692 (3); 8093 (3); 8113 (11); 8168 (11); 8201 (5); 8207 (3); 8212 (5); 8267 (3); 8395 (14); 8426 (3); 8604 (14); 8644 (3); 8688 (11); 8777 (3); 8819 (5); 8822 (16); 8834 (15); 8920 (3); 8935 (3); 8940 (16); 9325 (5); 9358 (2); 9488 (5); 9497 (5); 9553 (3); 9607 (3); 9742 (9); 9744 (3); 9764 (14); 9785 (3); 73747 (6); 73774 (3); 73899 (8).
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C.K. Schneider: 2732 (14).
H. Sun et al.: 1372 (5); 1654 (5); 1655 (3); 1656 (3).

Tha Hla: 3955 (3).
Tsai: 54255 (14); 54376 (1); 54459 (1); 54470 (5); 54487 (3); 54529 (5); 54551 (10); 55714 (8); 55729 (8); 55775 (8); 55880 (5); 56561 (1); 56679 (10); 58706 (14); 58808 (5); 58843 (14); 58847 (5); 59127 (2).
Wang: 66613 (5); $66662(5) ; 66890(11) ; 67551$ (14); 88262 (14); 89739 (3); 89818 (3); 89869 (6); 90011 (1); 90066 (1); 90118 (1); 90160 (1); 90165 (3); 90588 (5); 90703 (5).
Wu: 6692 (13); 6752 (3); 6762 (3); 6830 (8); 6893 (3); 7098 (3); 7123 (3); 8006 (3); $8020(3) ; 8022(11) ; 8105$ (11); 8125 (3); 8217 (3); 8290 (11); 8363 (3); 8766 (5); 9040 (14); 9155 (5); 9241 (14); 9280 (5); 10013 (14); 24125 (3); 24558 (3).
D.Y. Xia: 7 (3); 74 (3); BG22 (5); 23 (5); 32 (11).
L.S. Xie: 817 (5); 877 (3).
S.X. Yang: 831 (8).
W.C. Yin: 1012 (8); 1227 (8); 601280 (6); 601296 (11); 601339 (5); 601340 (14); 601383 (1).

Yü: 19400 (3); 19904 (3); 19946 (16); 19994 (3); 20119 (14); 20862 (16); 20972 (14); 22104 (14); 22960 (14); 22961 (14); 24211 (9).
J.Z. Zhao: 59 (6).

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# Two New Grenadiers (Teleostei, Gadiformes, Macrouridae) from the Seychelles and Mascarene Ridge, Western Indian Ocean 

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#### Abstract

Coelorinchus yurii and C. amirantensis are newly described from the western Indian Ocean. They belong to the group of Coelorinchus having a small ventral light organ that is not visible externally, anus immediately before anal fin, long pointed snout with anterolateral margin not completely supported by bone, coarsely spined head ridges, notably heavy scales with bladelike spinules in high ridge-like rows, and underside of head completely or almost completely scaled. Coelorinchus yurii is similar to C. lasti and C. kermadecus, but differs in several squamation and proportional features. Coelorinchus amirantensis is similar to C. trachycarus, but differs in ground color, squamation, and a few head proportions. The two new species add to the more than 100 species of Coelorinchus currently recognized.


During a December 1998 cruise of the R/V Sea Surveyor, a three-walled monofilament trammel net was set at a depth of 1900 m between the islands of Alphonse and Bijouteire, Seychelles. After an overnight soak, the net was hauled aboard with the catch (Fig. 1), which included three grenadiers of the genus Coelorinchus and three damaged specimens of Corypiciu... 15 , a 229 cm TL specimen of Pseudotriakis microdon, a 116.5 cm TL specimen of Centroscymnus coelolepis, and some geryonid crabs. The two sharks were recorded by Baranes (2003) and the crabs by Galil and Manning (2001) (who mistakenly reported the depth as 1400 m ). The three Coelorinchus specimens represented two undescribed species, which we herein describe.

The two new Coelorinchus species were previously captured off the Mascarene Ridge to the southeast of the Seychelles by the former Soviet Union research vessels Fiolent and Zvezda Kryma in 1976 and 1977, and the Vityaz' II in 1989. It had been the intent since 1988 of the first author and Yuri N. Shcherbachev (P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences) to collaborate in describing the two species, but diversions from other projects interfered with completion of this effort. Owing to recent medical problems, Shcherbachev is no longer able to work on this project. We therefore name one of these two species after Shcherbachev to recognize his contributions to the knowledge of Indian Ocean grenadiers and other deepwater fishes.

## Materials and Methods

Type specimens are deposited in the following institutions, whose abbreviations follow that proposed by Leviton et al. (1985) and Leviton and Gibbs (1988): California Academy of Sciences (CAS); Zoological Museum, Tel-Aviv University (TAU); Zoological Museum, Moscow State

University (ZMMGU). Methods for taking counts and measurements follow procedures described by Iwamoto and Sazonov (1988). In the descriptions, the characteristics or values for the paratypes are enclosed in parentheses.

The trammel net used to capture the fishes is a type used by commercial fishermen in the Mediterranean. The three walls of the net are each 50 m long and 2 m high; the outer two nets are of 150 mm mesh, the middle net of 40 mm mesh. The net was baited with small fish in perforated plastic bags tied to the net. A small boat ( 7 m long) was used to cast the net, which was weighted to keep it on the ocean floor and connected by a long line to a buoy on the surface.

## Coelorinchus yurii Iwamoto, Golani, Baranes, and Goren, sp. nov.

Figures 2-3
Type specimens.- Holotype: TAU P. 11602 ( 154 mm head length, $541+\mathrm{mm}$ total length); Seychelles between Alphonse and Bijoutier islands; by trammel net in 1900 m ; 17 Dec. 1998; collector M. Goren. Paratypes: CAS 66472 ( 2, , $84.7-94.3 \mathrm{~mm}$ HL, 275+-313 mm TL); Mascarene Ridge, off Saya de Malha Bank; $8^{\circ} 32^{\prime} \mathrm{S}$, $59^{\circ} 41^{\prime} \mathrm{E} ; 960-1130 \mathrm{~m} ;$ R/V Vityaz' II cr. 17, st. 2820; 29-m otter trawl; 10 Jan. 1989. ZMMGU uncat. (7, 71-92.6 HL, 249+-375+ TL) and CAS 223466 (3, 72.0-76.5 HL, 245-290 TL); Mascarene Ridge, Saya de Malha Bank; $9^{\circ} 32.7^{\prime}$ S, $60^{\circ} 02^{\prime}$ E; 800 m ; R/V Fiolent cr. 7, trawl 156; 26 Sept 1977. ZMMGU uncat. (84.7 HL, 250+ TL); Mascarene Ridge, Saya de Malha Bank; $9^{\circ} 51^{\prime} \mathrm{S}, 60^{\circ} 18^{\prime} \mathrm{E} ; 820 \mathrm{~m}$; $R \mathrm{~V}$ Fiolent cr. 7, trawl 156A; 26 Sept. 1977.

Diagnosis.- Snout 2.1 to 2.5 times into HL, 1.4 to 1.8 times orbit diameter, acutely pointed in lateral and dorsal views, its anterolateral margin not completely supported by bone; light organ small, not externally visible; underside of snout covered with tiny scales having 1 to 4 short, conical to bladelike spinules; nasal fossa naked except for few scattered tiny scales near ventral border; body scales large, $3 \frac{1}{2}$ to $4 \frac{1}{2}$ rows between lateral line and mid-base of first dorsal fin, exposed field of largest scales on dorsum beset with small spinules aligned in 6 to 8 more-or-less parallel rows, the middle row slightly enlarged so as to give appearance of fine longitudinal striations on body; interspace between dorsal fins short, usually less than (but sometimes slightly more than) length base of first dorsal fin; head ridges armed with heavy, coarsely spinulated scales; overall coloration dark brown in large adults, light brown in smaller ( $<100 \mathrm{~mm} \mathrm{HL}$ ) specimens; fins all blackish.

Counts (see Table 1 for measurements).- 1D. II,8 (8-9); P. i, 18 (i,16-18); V. 7; inner gill rakers first arch $2+6(2+5-7$; 7 or 8 total), second arch (outer/inner) $0+6 / 2+6(0-1+5-6=5-7$ total $/ 1-2+5=7$ or 8 total); scales below origin of 1D. 5 (4.5-5.5), below mid-base of 1D. 4.5 (4.0-4.5); below origin of 2D. 5.5 ( $4.5-5.5$ ); pyloric caeca ( $11,1 \mathrm{spec}$. ).

Description.- Head large, broad, length about 3.5 (3.3-4.5) into total length, width about equal to greatest body depth or postrostral length of head. Body deepest under origin of first dorsal fin, tapering fairly rapidly behind anus to long tail. Trunk moderately long, about three-quarters length of head. Snout acutely pointed, tipped with a broad, somewhat diamond-shaped terminal scute. Orbits large, about 1.7 (1.4-1.8) into snout length, slightly less than (0.9-1.1) interorbital width. Suborbital region broad, with a stout, bony, longitudinal ridge passing from tip of snout to posterior angle of preopercle dividing head into dorsal and ventral parts. Dorsal surface of suborbital almost vertical (to inclined laterally), the lower surface below suborbital ridge sharply inclined mesially. All ridges of head strong, consisting of stout, thick, scute-like scales armed with short, conical spinules. Mouth broad, gape little restricted at posterior angles of jaws; posterior edge of maxilla below posterior one-fourth or less of orbit; anterior end of jaws below anterior nostril; posterior nostril large, greatest diameter about 2.8 into greatest orbit diameter. Nasal fossa large, circumference with strong, adherent scales, but almost all fossa surface naked except for scattered tiny scales at anteroventral end (entirely naked in paratypes). Preopercle large, hind margin inclined at about $60^{\circ}$ angle, forming moderately angular lobe at posteroventral corner, beyond which extending slender narrow tip of subopercle. Interopercle completely covered by preopercle. Gill membranes connected across isthmus, with a slight free fold; gill opening extending ventrally to vertical under preopercle. Chin barbel short and slender, its length about 2.4 (2.8-4.2) into orbit diameter. Gill rakers short, tubercular; gill filaments of moderate length; outer and innermost gill slits restricted by folds of skin attached to upper and lower ends of gill arch, as typical for all members of genus. Light organ short, not externally visible.

Teeth in short, fairly uniformly wide band; smaller inner teeth about three rows deep and a single outer series of slightly larger teeth. Mandibular teeth all small, conical, in rather narrow band


Figure 2. Coelorinchus yurii sp. nov. Holotype, TAU P. 1602 ( 154 mm HL, $541+\mathrm{mm}$ TL), from 1900 m in the Amirantes Basin, Seychelles. (a) Lateral view; (b) dorsal view of head; (c) ventral view of head and trunk.
about three to four rows deep. Premaxillary tooth band extends laterally only about two-thirds length of rictus; mandibular tooth band extending to near end of rictus.

First dorsal fin short based, fairly high, length of second spinous ray 2.1 (1.5-2.3) into head length, its tip fine and scarcely extending beyond first segmented ray. Longbased second dorsal fin low to end of tail. Anal fin deep throughout its length. Pectoral fin relatively short, narrow based, tip falling short of vertical through (slightly beyond) anal-fin origin. Pelvic fin

Table 1. Comparison of selected measurements and counts of Coelorinchus yurii and C. amirantensis. Values in parentheses represent those of the holotypes; proportional measurements are in percent of HL.

| Character | C. amirantensis | C. yurii |
| :--- | :---: | :---: |
| Total length (mm) | $149-525+$ | $245-375+(541+)$ |
| Head length (mm) | $41-157(157)$ | $71-154(154)$ |
| Snout length (\%HL) | $46-51(47)$ | $41-44(42)$ |
| Internasal width (\%HL) | $17-20(18)$ | $18-21(19)$ |
| Interorbital width (\%HL) | $20-24(23)$ | $20-24(26)$ |
| Orbit diameter (\%HL) | $21-25(23)$ | $24-29(24)$ |
| Suborbital width (\%HL) | $12-16(15)$ | $13-14(17)$ |
| Postorbital length (\%HL) | $29-33(33)$ | $30-34(37)$ |
| Length orbit-preop. (\%HL) | $29-34(34)$ | $32-35(40)$ |
| Length upper jaw (\%HL) | $20-23(23)$ | $22-26(31)$ |
| Barbel length (\%HL) | $4-7(4)$ | $6-9(10)$ |
| Length 1st gill slit (\%HL) | $9-13(13)$ | $9-12(14)$ |
| Body depth | $34-47(47)$ | $45-54(62)$ |
| Height 1D | $27-39(29)$ | $43-67(47)$ |
| Length base 1D | $9-13(15)$ | $17-21(16)$ |
| 1D-2D interspace | $9-15(14)$ | $18-30(16)$ |
| Length P | $27-39(29)$ | $-37-42(41)$ |
| Length V | $27-32(31)$ | $34-41(41)$ |
| Lateral-line scales over pre-1D length | $35-40$ | $27-33(40)$ | narrow based, its outer ray hair fine at tip and extending to anus (to third or fourth anal-fin ray).

All scales strong and adherent, those on body large; those under origin of second dorsal fin with spinules in roughly 8 to 12 (6-8) irregularly parallel rows (Fig. 3a); middle row of spinules slightly enlarged, giving appearance of horizontal striations on body surfaces, especially on flanks and tail, less so on anterior parts of trunk and nape, where spinules rows divergent. Lateral rows of spinules usually short, some with only 2 or 3 spinules per row, and often incomplete, usually falling short of posterior edge of scale. Anterior spinules much smaller and more slender than those along posterior margin of scale. Spinules narrowly triangular, somewhat trihedral in cross section, with prominent transverse buttresses on each side of base; spinules reclined almost 30 degrees from horizontal and overlapping, with lateral buttresses of two or more spinules in adjacent rows often joined, sometimes forming concentric series of low ridges across exposed field of scale (buttresses little developed and not joined in paratypes, which are much smaller than holotype). Scales more posteriorly on tail with spinules more slender; buttresses less extensive with fewer joined to those of adjacent spinules. Head scales strong, greatly variable in size, most of those in occipital region, on parts of preopercle, and alongside supranarial ridge largest, covered with widely divergent rows of small, short spinules: scales on interorbital space between occipital ridges with short spinules in slightly divergent rows. Areas immediately above and behind leading edge of snout with small scales beset with short, erect, somewhat conical spinules; other areas of dorsal and lateral surfaces of head intermixed with small and large scales. Underside of head and mandibular rami almost fully covered with small, non-imbricate scales (Fig. 3b), except for a median swath of naked skin on lower surface of snout (scales confined to lateral margins of snout in some paratypes); these scales armed with one to four erect spike-like or blade-like spinules; naked swath covered with slender, pointed, black papillae, most ranging 0.6 to 1.6 mm long (smaller in paratypes). Head ridges all strongly and stoutly armed with coarse scute-like scales having short, conical spinules; scales on supranarial ridge notably broad, with spinule rows in a radial pattern. Supraoccipital and postoccip-


Figure 3. Coelorinchus yurii sp. nov. (a) Scale from dorsum between second dorsal-fin origin and lateral line; (b) scale from underside of head.
ital scutes stout and coarsely spinulated. Scales along outer margin of gill cover end abruptly, with none actually covered by gill membranes. Branchiostegal and gular membranes naked.

Color uniformly dark brown (medium to light brown in paratypes, which are much smaller than holotype); color of abdomen like that of remainder of trunk and not darker (bluish in paratypes lacking scales over abdomen). Gular membrane somewhat darker (whitish in some paratypes), branchiostegal membranes blackish (dusky); lips black (pale). Fins all black (dusky in some). Eye ring and septum between nostrils black (blackish). Mouth pale to dusky; lining of gill cavity black.

Distribution.- Known only from the Seychelles and Mascarene Ridge in the western Indian Ocean, at depths of 800 to 1900 m .

Etymology.- The species is named in honor of Yuri N. Shcherbachev of the Institute of Oceanology, Russian Academy of Sciences, who initially recognized this species as new and had planned to describe it with the first author.

Comparisons.- Coelorinchus yurii falls in a group of Coelorinchus species characterized by the combination of small light organ, usually not externally apparent; anus immediately before analfin origin; snout long, orbit diameter usually 1.4 or more times into snout length; anterolateral margin of snout not completely supported by the nasal bone; underside of head completely or almost completely scaly; and no prominent body markings. The naked nasal fossa (except for a few scales ventrally in large holotype), large body scales, and characteristic spinulation on scales of body and head serve to distinguish the new species from all others of the genus. Coelorinchus yurii is similar in most features to C. kermadecus Jordan and Gilbert, 1904, a species of southeastern Australia and New Zealand, but the nasal fossa in C. yurii is not as extensively scaled as in C. kermadecus, the dorsal fin is slightly higher ( $43-66 \%$ HL in adults, cf. less than $45 \%$ ), and spinule rows on body scales are more numerous (usually $8-12 c f .3-7$ ) and not as widely divergent.

Coelorinchus lasti Iwamoto and Williams, 1999 shares many important characters with C. yurii, notably a dark-brown coloration in large adults, closely similar body proportions and counts, naked or sparsely scaled nasal fossa, and similar scale morphology and distribution of scales on head and body surfaces. However, the spinules on body scales are in 3-5 divergent rows in C. lasti and spinules on scales on the underside of the head are bladelike and in high ridgelike rows. The snout in adults of C. yurii is longer ( $41-48 \%$ of head length, cf. $37-38 \%$; preoral length $37-42 \%$, cf. 30-32\%).

The species is closely similar to the second new species Coelorinchus, here described, but differs in a number of proportional measurements, which are compared in Table 1. The scale spinules
in C. amirantensis are much broader overall than those in C. yurii, with higher buttresses that form a greater interconnection between adjacent scales (cf. Figs. 3a and 5a). This is most noticeable in the dorsal and ventral extremities of the exposed fields in scales on the trunk and tail. Overall, the squamation of $C$. yurii is less harsh than in C. amirantensis.

Remarks.- Many proportional measurements of the large holotype differed considerably from those of the much-smaller paratypes. Although somewhat troubled by this, we attribute these differences to size-related changes and assume that a graded size series will eventually show ontogenetic changes explaining the differences.

## Coelorinchus amirantensis Iwamoto, Golani, Baranes, and Goren, sp. nov.

Figures 4-5.
Type specimens.- Holotype: TAU P. 11600 ( 157 mm HL, tail incomplete); Seychelles between Alphonse and Bijoutier islands; by trammel net in 1900 m ; 17 Dec. 1998; collector M. Goren. Paratypes: TAU P. 11603 ( $139.6 \mathrm{HL}, 420+\mathrm{TL}$ ); same data as for holotype. CAS 223467 (3, 96-126.5 HL, 285+-374 TL) and ZMMGU uncat. (3, 109-124 HL, 347-417 TL); Mascarene Ridge, $8^{\circ} 26.4^{\prime} \mathrm{S}, 59^{\circ} 29^{\prime} \mathrm{E}$; $1300-1260 \mathrm{~m} ; ~ R / V$ Fiolent cr. 7, trawl 52; 2 Sept. 1977. ZMMGU uncat. (2, 41-79.7 HL, 149-265 TL); Mascarene Ridge, $8^{\circ} 07^{\prime} \mathrm{S}$, $59^{\circ} 18.6^{\prime}$ E; 1300-1240 m; R/V Fiolent cr. 7, trawl 53; 3 Sept. 1977. ZMMGU uncat. ( $84-145 \mathrm{HL}, 262+525+$ TL); Mascarene Ridge, $8^{\circ} 29^{\prime} \mathrm{S}$, $59^{\circ} 35^{\prime} \mathrm{E}$; 950-1200 m; R/V Zvezda Kryma, cr. 6, trawl 4; 19 June 1976. ZMMGU uncat. ( $81 \mathrm{HL}, 258 \mathrm{TL}$ ); Mascarene Ridge, $8^{\circ} 08^{\prime} \mathrm{S}$, $59^{\circ} 37.6^{\prime} \mathrm{E}$; $1247-1269 \mathrm{~m}$; R/V Zvezda Kryma, cr. 6, trawl 210.

Diagnosis.- Snout long, 2.0 to 2.2 times into HL, 2.5 times orbit diameter, acutely pointed in lateral and dorsal views, its anterolateral margin not completely supported by bone; light organ small, not externally visible; underside of snout covered with tiny scales having 1 to 4 short, conical to bladelike spinules; nasal fossa naked or with a scattering of tiny scales along ventral margin; body scales large, $41 / 2$ rows between lateral line and mid-base of first dorsal fin, exposed field of largest scales on dorsum beset with small spinules aligned in 6 to 10 more-or-less parallel rows, the middle row enlarged so as to give appearance of longitudinal striations on body; interspace between dorsal fins short, about equal to length base of first dorsal fin; head ridges armed with heavy, coarsely spinulated scales; overall coloration medium brown, fins all black or dark.

Counts (see Table 1 for measurements).- 1D. II, 7(7-8); P. i17 (i16-i18); V. 7; total inner gill rakers first arch 8 ( $7-8$ ), second arch (outer/inner) $6 / 8$ (6-7/7-8); scales below origin of first dorsal fin $5.5(4.5-6.5)$, below mid-base of first dorsal $4.5(3.5-4.5)$; below origin of second dorsal fin 4.5 (4.5-5.5); over distance equal to predorsal length (35-40).

Description. - Head large, broad, width across preopercles more than greatest body depth; (length 3.0-3.6 in TL). Body relatively shallow, tapering smoothly to end of tail. Snout long, (2.0-2.2 in HL), sharply pointed, depressed, tipped with a broad flat shield-shaped median scute. Orbit oval to oblate (about 1.8-2.3 into snout length, usually $1.0-1.1$ into interorbital width). Subopercular region broad, sharp longitudinal ridge separating upper and lower surfaces; ridge continuous from tip of snout to posterior angle of preopercle, ending in long, thick, spiny scute having one or two sharp spinules projecting posteriorly. Head ridges strong, with notably stout modified scales armed with short. coarse, sharp spinules. Mouth broad, its gape restricted by lip folds at posterior corner; maxilla extending to below posterior one-third of orbit. Nasal fossa large, naked area extending to modified scales of suborbital ridge, but a scattering of small scales along ventral margin of fossa (entirely or almost entirely naked in smaller paratypes). Preopercle large, its vertical margin inclined to form lobe; corner margins of preopercle somewhat crenulate. Subopercle produced posteriorly into slender tag protruding beyond preopercle. Gill membranes broadly connected across, and attached mesially to, isthmus, without a free fold. Gill opening ventrally closer to


Figure 4. Coelorinchus amirantensis sp. nov. Holotype, TAU P. 1600 ( 157 mm HL , tail incomplete), from 1900 m in the Amirantes Basin, Seychelles. (a) Lateral view; (b) dorsal view of head; (c) ventral view of head and trunk.
vertical through posterior end of preopercle than to orbit. Chin barbel short, its length much shorter than posterior nostril, about 5 times into greatest orbit diameter. Gill rakers short, tubercular or plate-like, none on outer side of first arch (as characteristic for members of genus). Free neuromasts on head and nape prominent (less so in smallest paratype), black; short black, hairlike papillae on underside of snout. Light organ short, not externally manifested.

Upper jaw teeth all small, in broad short cardiform band, tooth band spanning about half rictus length. Lower jaw teeth similarly all small, but in long narrow tapered band that extends to posterior end of rictus.

First dorsal fin relatively low, its greatest height about equal to postorbital length of head, much shorter than snout length; base short, about equal to interspace between first and second dorsal fins. Second dorsal fin low over most of length, higher posteriorly; anal fin well developed and much deeper than second dorsal fin.

All scales strongly adherent and coarsely spinulated. Head ridges strong, formed of stout, sharply spinulated, heavily modified scales. Body scales large, those on dorsum in area between dorsal fins and below origin of second dorsal fin (Fig. 5a) covered with high, blade-like, trihedral spinules with broad buttresses that interconnect with buttresses on adjacent spinules. Individual spinules broadly triangular or shield-shaped, each with dorsal keel closely overlapped by spinule immediately anterior in position along each row. Rows more or less parallel along longitudinal axis, but rows often obscured by short spinule rows and high buttresses; about $8-10$ (6-8 in smaller paratypes) irregular rows in largest scales, with middle row largest and highest, producing distinctive striated appearance to body surfaces. Broad posteriormost spinules on scales usually extending well beyond posterior margin. Head scales highly variable in size and spinulation. Supraoccipital and postoccipital scutes stout and coarsely spinulated. Scales on interorbital space small, sparsely armed with broadly bladelike, erect, non-imbricate spinules. Those over dorsal surfaces of snout similar but with more numerous spinules aligned in slightly divergent rows. Ventral surfaces of snout almost completely covered with small non-imbricate scales, each armed with few short, erect,


Figure 5. Coelorinchus amirantensis sp. nov. Scale from (a) dorsum between second dorsal-fin origin and lateral line, and (b) from underside of head.
spikelike to bladelike, trihedral spinules (Fig. 5b); small triangular area immediately before mouth naked (naked area larger in smaller paratypes). Scales along gill cavity ending abruptly, none covered by gill membrane.

Color overall light to medium brown, darker and somewhat swarthy over abdomen and tinged with blue; gill membranes, lips, posterior half of operculum, eye ring, external jaw membranes, and fins black (blackish). Underside of head, jaws, mouth, and gill cavities dark (medium brown in smaller paratypes). Base of pectoral fins, especially mesially, dark, almost black. Outer rim of posterior nostril black edged.

Distribution.- Known only from the Seychelles and Mascarene Plateau in the western Indian Ocean, at depths of 950 to 1900 m .

Etymology.- The species name is derived from the Amirantes Basin, the type locality of the species.

Comparisons.- Specimens of this new species are very reminiscent of C. trachycarus Iwamoto, McMillan, and Shcherbachev, 1999 from the Tasman Sea and southern Australia, especially in the harsh, coarse, scale spinules on the body and on head ridges, in the dark overall color of membranes and fins, and in most proportions. The body color is paler, however, and lacks the distinctive purplish tinge in the integument of that species. The snout is longer as a proportion of the orbit, and the postorbital and interorbital proportions differ. Scale spinules are also much broader overall and in fewer rows. Naked areas along the suborbital and the lower preopercular margins are less than in $C$. trachycarus. Proportional differences include orbit into postorbital 1.2-1.5 in $C$. amirantensis cf. 1.0-1.2 in C. trachycarus, orbit into snout 1.8-2.1 cf. 1.4-1.9.

The species is very similar to another apparently undescribed species of Coelorinchus with which it apparently co-occurs on the Mascarene Ridge. Coelorinchus amirantensis differs from that species in having coarser, more spiny scales, and a slightly broader snout with lateral contours more convex. Differences between this third undescribed species, which Yuri Shcherbachev recognized as new, have not been adequately investigated. Its description awaits further examination of specimens and documentation of diagnostic characters.

## Discussion

The discovery of two (and possibly three) undescribed species of Coelorinchus from the Seychelles and the Mascarene Ridge to the southwest is indicative of the scant collecting efforts conducted on oceanic elevations in the tropical western Indian Ocean. The few deepwater trawl col-
lections available from such areas are almost exclusively those made by the former Soviet Union in the 1970s and 1980s. Shcherbachev (1987) provided a preliminary list of the thalassobathyal fishes collected in the subtropical and tropical Indian Ocean. He and his Russian colleagues, including (the late) Y.I. Sazonov, N.V. Parin, A.S. Piotrovsky, and N.P. Pakhorukov, published numerous articles describing the grenadiers and other deepwater fishes from those collections (for a partial list, see the literature citations in Shcherbachev and Iwamoto 1995).

In 1988 Iwamoto, Sazonov, and Shcherbachev began a collaborative effort to report on all of the grenadiers from the Indian Ocean. Several papers resulted from that collaboration and the genera Coryphaenoides (Iwamoto and Shcherbachev 1991, Shcherbachev and Iwamoto 1995), Kumba (Iwamoto and Sazonov 1994), and Kuronezumia (Shcherbachev et al. 1992) were treated in depth. One article describing a new species of Coelorinchus from Walters Shoals (Iwamoto et al. 2004) was the last of such collaborations. The most specious genus, Coelorinchus, the bathygadines, the genus Nezumia, and several minor genera were left untreated. It is apparent that many Indian Ocean grenadiers, especially in the genus Coelorinchus, remain undescribed or unrecorded.

The capture of the three large specimens of Coelorinchus in the Seychelles using a trammel net fished at depths much greater than those fished by Soviet trawlers off the Mascarene Ridge suggests an effective means by which large grenadiers can be collected at great depths. Use of such nets is much less expensive in terms of vessel and equipment costs and is probably more effective than bottom trawls, longlines, and traps for grenadiers in rough-bottom areas. The size of vessels used for such work can be relatively small, with limitations dictated primarily by proximity to ports and prevailing oceanographic conditions.

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## Literature Cited

Baranes, Albert. 2003. Sharks from the Amirantes Islands, Seychelles, with a description of two new species of squaloids from the deep sea. Israel Journal of Zoology 49:33-65.
Galil, Bella S., and Raymond B. Manning. 2001. A new geryonid crab from the Amirante Basin, western Indian Ocean (Crustacea: Decapoda: Brachyura). Proceedings of the Biological Society of Washington 114 (1):104-108.

Iwamoto, Tomio, and Yuri I. Sazonov. 1988. A review of the southeastern Pacific Coryphaenoides (sensu lato) (Pisces, Gadiformes, Macrouridae). Proceedings of the California Academy of Sciences, ser. 4, 45(3):35-82.
Iwamoto, Tomio, and Yuri I. Sazonov. 1994. Revision of the genus Kumba (Pisces, Gadiformes, Macrouridae), with the description of three new species. Proceedings of the California Academy of Sciences, ser. 4, 48(11):221-237.
Iwamoto, Tomio, a.vd Yuri I. Shcherbachev. 1991. Macrourid fishes of the subgenus Chalinura, genus Coryphaenoides, from the Indian Ocean. Proceedings of the California Academy of Sciences, ser. 4, 47(7):207-233.
Iwamoto, Tomio, Yuri N. Shcherbachev, and Bryan Marquardt. 2004. Grenadiers (Gadiformes, Teleostei) of Walters Shoals, southwestern Indian Ocean, with description of a new "West-Wind Drift" species. Proceedings of the California Academy of Sciences 55(10):190-307.
Leviton, Alan E., Robert H. Gibbs, Jr., Elizabeth Heal, and Charles E. Dawson. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetol-
ogy and ichthyology. Copeia 1985(3):823-832.
Leviton, Alan E., and Robert H. Gibbs, Jr. 1988. Standards in herpetology and ichthyology. Standard symbolic codes for institution resource collections in herpetology and ichthyology. Supplement no. 1: additions and corrections. Copeia 1988(1):280-282.
Shcherbachev, Yuri N. 1987. Preliminary list of thalassobathyal fishes of the tropical and subtropical waters of the Indian Ocean. [In Russian.] Voprosy Ikhtiologii (1):3-11. [English version in Journal of Ichthyology 27(2): 37-46]
Shcherbachev, Yuri N., and Tomio Iwamoto. 1995. Indian Ocean grenadiers of the subgenus Coryphaenoides, genus Coryphaenoides (Macrouridae, Gadiformes, Pisces). Proceedings of the California Academy of Sciences, ser. 4, 48(14):285-314.
Shcherbachev, Yuri N., Yuri I. Sazonov, and Tomio Iwamoto. 1992. Synopsis of the grenadier genus Kuronezumia (Pisces: Gadiformes: Macrouridae), with description of a new species. Proceedings of the California Academy of Sciences, ser. 4, 48(3):97-108.

# A New Species of Pseudocerastes with Elaborate Tail Ornamentation from Western Iran (Squamata: Viperidae) 

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#### Abstract

A new species of viper, Pseudocerastes urarachnoides, is described from the Zagros Mountains in western Iran. The new species has a short tail, few pairs of subcaudals ( 15 in the known specimens), the distal pairs forming an oval knob-like structure; lateral dorsal caudal scales projected to form elongate "appendages" along the sides of the terminal knob. Several rows of lateral dorsal scales are weakly keeled and outer rows are only faintly keeled. We speculate that the caudal appendage may serve as a lure for prey in an ambush predator.


Keywords: Pseudocerastes urarachnoides, Pseudocerastes persicus, Pseudocerastes fieldi, new taxon, Iran, caudal lure, caudal ornamentation, Viperidae

The Second Street Expedition to Iran (1968) collected amphibians and reptiles incidental to the mammals that were the primary objectives. These specimens were deposited in the Field Museum of Natural History, where one of us (SCA) examined and identified them in 1970. The first impression of FMNH 170292, seen through the bottle in the preparations room, was that a small solpugid was clinging to its tail. Subsequent examination revealed that the snake was a specimen of Pseudocerastes with a peculiar growth at the tail tip. It was identified as $P$. persicus, with which it agreed in most particulars. As there was only the single specimen, it was not possible to say whether the pecular growth of the tip of the tail had a genetic origin or was, perhaps, some sort of tumor or caused by some parasite. Thus, the specimen languished, but was not forgotten, for nearly four decades. Then, in 2003, one of us (HB) collected a second specimen with identical tail ornamentation and similar scale counts and morphology. It seems likely that there has been genetic continuity in this character over the past 35 years. Were the caudal appendage the result of a characteristic tumor or due to the action of a parasite, we might expect it to have been observed elsewhere and, perhaps, in other species. We believe that these two specimens represent an undescribed species, related closely to Pseudocerastes fieldi and P. persicus. This appears to be the most elaborate morphological caudal ornamentation yet reported in a snake, with the possible exception of the rattles of Crotalus and Sistrurus.

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## Pseudocerastes Boulenger, 1896

Type species: Cerastes persicus Duméril, Bibron, and Duméril, 1854, by monotypy
Definition.- Head distinct from neck, covered with small scales; pupil of eye vertical; nostril directed outwards and upwards, in large undivided nasal shield (pierced between two small scales, a larger crescentic anterior and a smaller scale-like posterior [Gasperetti 1988:350]) (nasal aperture in a large circular or crescentic shield, the upper part of the aperture leading into the supranasal sac [Smith 1943:490, fig. 155A]); supralabials with serrated lower margin and with inner groove to receive lower lip (The structure of the lips, to provide complete closure of the mouth, and the valvular prominence within the nasal aperture, are typical desert modifications against the ingress of blown sand. They are found also in Eristocophis [Smith 1943:490]); body scales in 21-25 longitudinal rows, none obliquely disposed; keels on body scales do not reach posterior edge of scale but end in swollen knob before outer edge, keels not serrated; ventrals rounded, without lateral keels; tail short, subcaudals paired (Leviton et al. 1992:114-115).

Distribution.- The North Arabian Desert from Sinai and southern Israel, Jordan, Iraq, southwestern Iran east to Afghanistan and Pakistan west of the Indus River, outlying population in northern Oman. (Fig. 13).

We include here brief descriptions of the previously recognized taxa of Pseudocerastes for comparison with the new species. Some authors have considered $P$. fieldi a subspecies of $P$. persi$c u s$. There appears to be a geographic hiatus in the distribution of the genus, $P$. persicus and $P$. fieldi nowhere known to be parapatric, their ranges separated by the Zagros Mountains. For this reason and the differences in venom properties (see below), we prefer to recognize them at the species level.

## Pseudocerastes persicus (Duméril, Bibron, and Duméril, 1854)

Cerastes persicus Duméril, Bibron, and Duméril, 1854:1443, pl. 78b.
Description (From Smith 1943:490-492, fig. 155).— Head depressed, snout short and broadly rounded; diameter of the eye less than its distance from the mouth; nostril very large, pierced in a large circular or crescentic nasal, bounded above by a supranasal which may be broken up; two scales between the nasal and the rostral; scales on top of the head small, imbricate, smooth on the snout, keeled behind in the young, tuberculate and more strongly keeled in the adult; an erect hornlike scale above the eye surrounded by small scales; 9-12 scales on a line between the horns; 16-20 scales round the eye; 3-4 scales on a line between the eye and the nasal; temporal scales small, keeled; 13-14 supralabials, 4 series of scales between them and the eye, 1st pair of infralabials larger than the others; a pair of large anterior genials, the scales posterior to them being much smaller.

Scales in 23 or $25: 23$ or 25 : 19 rows, striated and strongly keeled, the outermost scales strongly overlapping the ventral scales. V 144-158; C 34-49, paired.

Hemipenis short, extending to the 8th caudal plate, deeply forked; the distal end is calyculate, the remainder spinose, the largest spines being at the proximal end; sulcus lips also spinose.

Snout-vent length 688-690 mm, tail $80-85 \mathrm{~mm}$.
Grayish-brown above, with squarish. dark brown, black-edged spots, which alternate with one another on either side of the vertebral line, or are confluent to form cross-bars; sides of the body with rounded, less distinct spots; top of the head pale grey, upper lip and side of the head darker, the two colors meeting in a sharply defined line which extends from the eye to the angle of the mouth: whitish beneath, spotted with brown. In the adult the markings are much less distinct and may be almost entirely absent. In large adults, tip of tail often dark. An adult from Kacha,

Baluchistan, is heavily marked and mottled with black and cream.
Total length: 890 mm ; tail 110 mm .
Distribution.- Southeastern Anatolia, Turkey and Iran east of the Zagros Mountains through the Iranian Plateau to central Afghanistan and western Pakistan (Fig. 13). Gasperetti (1988:353, fig. 127) shows four localities in northern Oman and the Musandam Peninsula.

Note.- Wall (1913:64) described Pseudocerastes bicornis from Khajuri Kach, Waziristan, Pakistan, based on a single specimen now in the Natural History Museum, London. The specimen consists of the head and anterior one-fourth of the body (Smith 1943:492). Subsequent authors (Minton 1966; Mertens 1969; Gasperetti 1988) have placed it in the synonymy of $P$. persicus, although Khan (2002:190) regards it as distinct. It must be noted that were the two specimens here described as a new species missing the tails, they would be identified as $P$. persicus.

## Pseudocerastes fieldi Schmidt, 1930

Pseudocerastes fieldi Schmidt, 1930:227, fig. 2 (Type locality: Ayn Bair, Jordan).
Description. - Head depressed, snout is very short and broadly rounded; diameter of the eye less than its distance from the mouth; nostril very large, pierced in a large circular or crescentic nasal, bounded above by a supranasal which may be broken up; two scales between the nasal and the rostral; the upper head scales are small, imbricate, keeled; there is an erect horn-like tubercle above each eye, covered with several imbricate scales; 9-12 scales on a line between the horns; 15 scales around the eyes; one or two series of scales between the nasal and the rostral; scales on top of the head small, imbricate, smooth on the snout, keeled behind; scales on top of the head small, imbricate, smooth on the snout, keeled behind; 13 supralabials, three series of scales between the eye and the labials; four infralabials in contact with the chin shields (genials). 1st pair of infralabials larger than the others; a pair of large anterior genials, the scales posterior to them being much smaller. Dorsal scales are strongly keeled in 21-23 rows; ventrals 134-138; the anal is entire, subcaudals, 35-38, divided (Schmidt's type had 21 dorsal scale rows, 134 ventrals, 35 subcaudals); total length 890 mm , tail $110 \mathrm{~mm}, \mathrm{TL} / \mathrm{T}=6.1-8.6$.

Colors are grayish or brownish above with four series of large dark spots, the two median rows sometimes confluent and forming cross bars; a dark streak on each side of the head from the eyes to behind the gape; the under parts are whitish, dotted with dark and a lateral series of dark spots. (Schmidt 1930:227-229; Gasperetti 1988:352-354, Table15).

Distribution.- Sinai, Israel, Jordan, Syria, Iraq, southwestern Iran (Fig. 13). The specimen cited by Anderson (1963:472) from Binak, Iran, upon reexamination, is identified here as $P$. fieldi (table 1).

Note.- Probably the main external morphological difference between P. persicus and P. fiel$d i$ is that the scale rows of $P$. persicus are all strongly keeled, whereas in $P$. fieldi several lateral rows are nearly smooth and the outer rows are entirely without keels. Pseudocerastes fieldi also has a significantly shorter tail. Sexual dimorphism has not been studied adequately in either taxon.

Bdolah (1986) demonstrated that the composition and properties of the venoms of P. fieldi and persicus differ greatly. The venom of $P$. persicus showed the typical complexities of most viperid snake venoms with potent hemorrhagic activity whereas that of $P$. fieldi demonstrated none. The venom of $P$. persicus has a yellow pigment typical of most snake venoms and that of $P$. fieldi is completely lacking in yellow flavin pigment and its isoelectric focusing profile is a simple one with very few protein bands. Pseudocerastes persicus, on the other hand, had close to 30 protein bands spanning a wide pH range. It was concluded that these differences indicate a long genetic separation of the two forms (Bdolah 1986:726) (Gasperetti 1988:352-353).

The tail tip is often dark in adults of both taxa, suggesting the possibility of caudal luring. (Gasperetti 1988:354, Table 15).

## Pseudocerastes urarachnoides Bostanchi, Anderson, Kami, and Papenfuss, sp. nov.

 Figures 1-12.Material examined.- Holotype: FMNH 170929 [ ${ }^{\circ}$ ], Iran: Ilam Province: 70 km SW Ilam [probably on road to Amirabad and Mehran], collected by Daniel R. Womochel and Anthony F. DeBlase, Second Street Expedition to Iran, 27 August 1968 (see map, Fig. 13). Paratype: ZMGU [ ${ }^{\circ}$ ], 1300, Iran: Kermanshah Province: 25 km south of Qasr-e-Shirin on road to Gilan-e Gharb, open level area in agricultural region, ca. 200 meters elevation, collected by Hamid Bostanchi, May 15, 2001 at about 0800 hrs (see map, Fig. 13).

Diagnosis.- A Pseudocerastes with a short tail ( $\mathrm{TL} / \mathrm{T}=9.65$ ), few pairs of subcaudals ( 15 in the known specimens), the distal pairs forming an oval knob-like structure; lateral dorsal caudal scales projected to form elongate "appendages" alongside terminal knob. Several rows of lateral dorsal scales are weakly keeled.

Description of holotype (FMNH 170929 \&, [Figs. 1-2, 8, 10]; head scales based on paratype, ZMGU $1300 \sigma^{2}$ [?] [Figs. 5-7, 9]).— The head of the holotype is severely damaged and accurate counts of many of the head scales are not possible; consequently the description of miss-


Figures 1-4. (1) Holotype, FMNH 170929, dorsal view (SCA photo). (2) Holotype, FMNH 170929, ventral view (SCA photo). (3) Paratype, ZMGU 1300, dorsal view (James Parham photo). (4) Paratype, ZMGU 1300, ventral view (HGK photo).
ing head characters is based on the paratype. Head depressed, snout short and broadly rounded; the upper head scales small, imbricate, keeled; there is an erect horn-like scale above the eye surrounded by small imbricate scales; 16 scales on a line between the horns; (Fig. 6); 17 scales around the eyes; three series of scales between the eye and the labials; two series of scales between the nasal and the rostral; 11/12 upper labials; 13/12 lower labials, 3-5 in contact with the chin shields; anteriormost lower labials enlarged, in contact behind mental and in contact with one pair of genials (fig. 7). Dorsal scales strongly keeled, in 21 rows at level of $6^{\text {th }}$ ventral, 23 rows at level of $73^{\text {rd }}$ ventral, 17 rows at level of $145^{\text {th }}$ ventral; several lateral rows are weakly keeled but the outer row is faintly, but distinctly keeled at midbody (Fig. 10); ventrals 145 ; the anal is entire, subcaudals 15 pairs; total length 531 mm , tail $55 \mathrm{~mm}, \mathrm{TL} / \mathrm{T}=9.65$.

Tail short, with only 15 pairs of subcaudals; dorsolateral caudal scales adjoining subcaudals have elongated keels, progressively longer from proximal to distal end of tail, keels of distal-most becoming entire scale, the longest measuring 11.2 mm ; tail terminates in an elongate, oval, bulb-like structure, measuring 10.4 mm , apparently formed of last pair of subcaudals, much enlarged, and a single enlarged dorsal scale; lateral scales elongated to the extent that they give the impression of arthropod legs (Figs. 8-9). The caudal vertebrae extend well into this structure and are not deformed or modified (Fig. 12).

Colors are grayish and brownish above with four series of large dark spots, the two median rows sometimes confluent and forming cross bars; a dark streak on each side of the head from the eyes to behind the gape; the under parts are cream, with a lateral series of dark spots (Figs. 1-4).

Remarks on paratype.- ZMGU 1300 is a juvenile, apparently male (see Table 1 for counts and measurements). The caudal ornamentation is less well developed (Fig. 9), possibly a factor of age.

The new species most closely resembles Pseudocerastes persicus in the dorsal scale characters which distinguish that taxon from $P$. fiel$d i$, apart from the greatly shortened tail and the elaborate caudal appendage, which set it apart from both. To the human observer this caudal appendage greatly resembles an arthropod clinging to the tail tip.

Unfortunately, neither specimen is in ideal condition, the head of FMNH 170929 having been severely damaged and ZMGU 1300 having partially rotted prior to proper preservation.

Figures 5-10. (5) Lateral view of head of Paratype, ZMGU 1300 (James Parham photo). (6) Dorsal view of head of paratype, ZMGU 1300 (HGK photo). (7) Ventral view of head of paratype, ZMGU 1300 (James Parham photo). (8) Tail ornamentation of Holotype, FMNH 170929 (SCA photo). (9) Tail ornamentation of paratype, ZMGU 1300 (HGK photo). (10) Ventrolateral scale rows keeled (holotype, FMNH 170929) (SCA photo).


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Derivation of name.- From the Greek: ura = tail; arachno $=$ spider; ides $=$ similar to.

Discussion and speculation.- This unusual snake occupies a region that lies between the recorded ranges of $P$. persicus and $P$. fieldii. Its discovery raises a number of interesting questions and speculations. Only one of us (HB) has seen this species alive, and while we speculate that the caudal appendage functions as a caudal lure, this remains to be verified. While anthropomorphic interpretation should be avoided where documentation is lacking, caudal luring is known for several species of snakes, e.g., Bitis caudalis, Crotalus cerastes, Sistrurus catenatus, Agkistrodon contortrix, Acanthophis antarcticus, Acanthophis praelongus, Morelia viridis, and others, and will probably be verified in many species with differentially colored tails. Gasperetti (1988:354) suggested that this might be the case for the previously known species of Pseudocerastes. Neill (1980) reviewed the literature on caudal luring in juvenile snakes, especially crotalids and boids, and suggested that the loss of contrasting tail color with age marked the transition from ectothermic prey (e.g., amphibians, lizards, scorpions, centipedes) to mammals. Greene (1992:111-112) added additional species to the list of snakes exhibiting caudal luring and suggested that contrasting


Figures 11-12. Radiographs of holotype showing undeformed caudal vertebrae extending into bulbus area of tail indicating that the tail tip was neither damaged nor regenerated. (Radiographs by Mark Zimmerman, FMNH.) tail coloring and luring behavior might be a synapomorphy in the Crotalinae, Viperidae, or larger clade. This raises the question of the elaborate and sophisticated appearance of the caudal appendage in our new species, as the waving or wriggling motion of a distinctively colored tail tip seems perfectly adequate to attract lizard and anuran prey. We can only speculate that in the case of the present species, the caudal lure serves to deceive a more specific kind of prey, such as shrews or birds. Indeed, ZMGU 1300 contains an undigested, unidentified passerine bird in the stomach (the feet protruding through the body wall). When sufficient specimens become available, additional stomach contents should be examined and observations made of the behavior of captive individ-


FIGURE 13. Map showing distribution of the genus Pseudocerastes (limits of distribution uncertain). (Map prepared by Karen Klitz.)

Table 1. Counts and measurements for specimens examined. ${ }^{7}$

|  | P. urarachnoides |  | P. persicus |  | P. fieldi |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | FMNH | ZMGU | Latifi |  | Latifi | CAS |  | CAS

[^1]uals. Latifi (1991:131) states that the diet of P. persicus consists of lizards and mice; Khan (2002) gives deserticolous lizards and arthropods as prey items.

As both available specimens were initially preserved in formalin, no tissue samples suitable for molecular analysis are available. Should such become available in the future, by comparing DNA from the three known species of Pseudocerastes, it may be possible to obtain a molecular clock estimate of the time required to evolve such a structure.

The venom of Pseudocerastes persicus and P. fieldi differ in their chemical composition and in their physiological action (Bdolah 1986:726), and it will be interesting to compare these with the venom properties of the new species, if and when the opportunity arises.

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## Literature cited

A.dderson, Steven C. 1963. Amphibians and reptiles from Iran. Proceedings of the California Academy of Sciences, ser. 4, 31(16):417-498, figs. 1-15.
Bdolah, AvNer. 1986. Comparison of venoms from two subspecies of the false horned viper (Pseudocerastes persicus). Toxicon 24(7):726-729, figs. 1-2.
Bollenger, George A. 1896. Catalogue of the Snakes in the British Museum (Natural History). Volume III.,

Containing the Colubridae (Opisthoglyphae and Proteroglyphae), Amblycephalidae and Viperidae. Trustees of the British Museum (Natural History), London, UK. xiv $+727+19$ pp., pls. 1-25.
Duméril, André Marie Constant, Gabriel Bibron, and Auguste Henri André Dumérll. 1854. Erpétologie Général ou Histoire Naturelle Complète des Reptiles, vol. 7 (part 2). Librairie Encyclopédique de Roret, Paris (1), (1), xii, 781-1536 pp., 2 folding tables, pls.83-84, pls. 75-84.
Gasperetti, John. 1988. Snakes of Arabia. Fauna of Saudi Arabia 9:169-450, 135 figs., 17 tables.
Greene, Harry W. 1992. The ecological and behavioral context for pitviper evolution. Pages 107-118 in J. A. Campbell and E. D. Brodie, Jr. eds. Biology of the Pitvipers. Selva Press, Tyler, Texas, USA.

Khan, Muhammad S. 2002. A Guide to the Snakes of Pakistan. English Edition. Edition Chimaira, Frankfurt am Main, Germany. 265 pp., 155 pls., 20 distribution maps.
Latifi, Mahmud. 1991. The Snakes of Iran, English ed. Contributions in Herpetology, 7. Society for the Study of Amphibians and Reptiles, Oxford, Ohio, USA. viii + 159 pp. 24 text-figs., 25 col. pls., 3 tables.
Latifl, Mahmud. 2000. The Snakes of Iran. 3 rd Persian ed. Tehran, Iran. 478 pp. (In Farsi)
Leviton, Alan E., Steven C. Anderson, Kraig K. Adler, and Sherman A. Minton, Jr. 1992. Handbook to Middle East Amphibians and Reptiles. Society for the Study of Amphibians and Reptiles, Oxford, Ohio, USA. 252 pp., unnumbered text-figs., 21 figs., 32 col. pls. 1 b\&w pl., 1 table.
Minton, Sherman A., Jr. 1966. A Contribution to the Herpetology of West Pakistan. Bulletin of the American Museum of Natural History 134(2):29-184, pls. 9-36.
Neill, Wilfred T. 1960. The caudal lure of various juvenile snakes. Quarterly Journal of the Florida Academy of Sciences 23(3):173-200.
Schmidt, Karl P. 1930. Reptiles of the Marshall Field North Arabian Desert Expedition, 1927-1928. Field Museum of Natural History, Zoological Series 12(13):221-230, figs. 1 [map] 2, pl. 2., figs. 1-2.
Smith, Malcolm A. 1943. Reptilia and Amphibia, vol. 3, Serpentes. The Fauna of British India, Ceylon and Burma, including the Whole of the Indo-Chinese Subregion. Taylor and Francis, London, UK. xii + $583+$ 5 pp., 166 figs., 1 fold-out map.

# PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES <br> Fourth Series 

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# On Palpibracus Rondani (Diptera: Muscidae) with Descriptions of New Species 

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#### Abstract

The distributions of all 16 currently recognized species of the Neotropical genus Palpibracus (Diptera: Muscidae) are restricted to Chile and Argentina. A large quantity of material of this genus, especially from Chile, was found in the collections of the California Academy of Sciences (San Francisco, California). Half of the known species of Palpibracus are represented in these collections, several of them by large series, as well as three new species, which are herein described - $P$. schlingeri (typelocality: Chile, Santiago), P. flavithorax (type-locality: Chile, Magallanes), and P. vittatus (type-locality: Chile, Cautin). Diagnoses and illustrations of the patterns of dorsum of mesonotum, pleurae and abdomen are presented for all studied species, and descriptions and illustrations of male and female terminalia are presented for the new ones.


Palpibracus is a Neotropical muscid genus, with its geographical distribution restricted to Chile and Argentina (Carvalho and Couri 2002; Carvalho et al. 2005; Soares and Carvalho 2005a). Palpibracus was proposed by Rondani (1864) as a replacement name for Brachypalpus Macquart, 1851 (preocc.). The original description included only one species - B. pilosus $[=P$. pilosus $]$ (Macquart 1851). Albuquerque (1951) proposed the synonymy of Darwinomyia Malloch with Palpibracus.

Among the most recent contributions to the taxonomy of the genus, Carvalho (1989a) presented a revision with redescriptions and illustrations of the species, whereas Lopes and Khouri (1996) and Pamplona and Couri (2000) each described a new species, respectively P. carvalhoi and P. valdiviensis, the latter transferred by Soares and Carvalho (2004) to Brachygasterina Macquart.

The systematic position of the genus was discussed by Carvalho (1989b) and Soares and Carvalho (2005b), who also described a new species, P. darwini. According to Soares and Carvalho (2005b), Palpibracus is a monophyletic genus, based largely on color characters, that is all of the species show beautiful shiny black and yellow patterns (shiny violet in $P$. lancifer) on both thorax and abdomen that are important taxonomic characters for their identification.

Soares and Carvalho (2005a) described areas of endemism for Palpibracus and analyzed its relationships based on three historical biogeographical methods.

According to the latest catalog of the Muscidae of the Neotropical region (Carvalho et al. 2005), Palpibracus includes 17 species - P. albuquerquei Carvalho, 1989; P. apicalis (Malloch, 1934); P. carvalhoi Lopes and Khouri 1996; P. chilensis (Bigot, 1885); P. confusus (Malloch, 1922), P. fasciculatus (Malloch, 1934); P. lancifer (Malloch, 1934); P. nigriventris (Malloch, 1928), P. peruvianus (Malloch, 1929); P. pilosus (Macquart, 1851); P. separatus (Malloch, 1934), P. similis
(Malloch, 1934), P. spicatus (Malloch, 1934); P. trivittatus (Malloch, 1934), P. univittatus (Bigot, 1857), P. valdiviensis Pamplona and Couri, 2000 and P. veneris (Bigot, 1888). To this list, three updates should be added: the transfer of $P$. valdiviensis to Brachygasterina (Soares and Carvalho 2004) and of P. apicalis to Psilochaeta, tentatively placed in this genus by Soares and Carvalho (2005b) and the inclusion of $P$. darwini, a new species also described in this latter reference.

The purpose of this contribution is to present the results of the study of the California Academy of Sciences Diptera collection, in which 11 species of Palpibracus were found, three of them new. Diagnoses and illustrations of the patterns of dorsum of mesonotum, pleurae and abdomen are presented for all studied species and descriptions and illustrations of male and female terminalia are presented for the new ones.

## Materials and Methods

The Diptera collection of the California Academy of Sciences (CAS, San Francisco, California) has a large quantity of unidentified material from southern South America. Most of the material was collected by M.E. Irwin and E.I. Schlinger in 1966 in Chile. For several of the species there are large series, which makes possible the observation of some color variation.

Holotype and paratype material of the new species and most of the material examined is deposited at CAS. Some specimens will be deposited at Museu Nacional, Rio de Janeiro collection (MNRJ) as indicated in the Material examined sections of the species descriptions.

Dissected terminalia were placed in glycerin in a microvial pinned with the respective specimen.

Color photos were made using Syncroscopy/JVC Auto-Montage with Leica M 420 optical microscope; drawings were made using an Olympus CH-2 optical microscope with camara lucida.

## Systematics: Descriptions and Redescriptions

A diagnosis of the genus and a discussion of its monophyly were published by Carvalho and Couri (2002) and more recently by Soares and Carvalho (2005b).

## Palpiracus carvalhoi Lopes and Khouri, 1996

Holotype. - Male, deposited at Museu Nacional (Rio de Janeiro, Brasil). Type-locality: Chile.

Diagnosis. - Palpus yellow. antennae brown, apex of pedicelum and base of flagellum yellow; frons reddish brown: female with interfrontal setae; katepimeron setulose; dorsum of mesonotum yellow with a median black central vitta. reaching the base of scutellum, a little larger than acrostichal row of setae but not reaching the dorsocentral row of setae; scutellum yellow with apex pale yellow (Fig. 1); pleurae with anepisternum, anepimeron, katepimeron and inferior half of meron brown; katepisternum and anterior and posterior spiracles yellow (Fig. 2); legs yellow with median third of fore femur brown: mid and hind femora with a brown ring on apical third; male legs: fore coxa without apical spine: mid femur with 4 weak setae on basal half; hind tibia slightly bent with fine anteroventral and posteroventral hairs; abdomen blackish brown with grayish pollinosity; abdomen as in Fig.3.

Color variatios.- The brown color on anepisternum, anepimeron, katepimeron and meron can be more or less extensive.

Material examined.- Chile: Concepcion: 1904, E.E. Reed collection (1 male,); Bio-Bio: El Abanico. Ross and Michelbacher. 30 December 1950 (2 males: 1 male, MNRJ); Santiago: Quebrada de la Plata Fundo. Rinconada. Maipu. $30^{\circ} 31^{\prime} \mathrm{S} 70^{\circ}+7^{\prime}$ W. 510 m . M.E Irwin, Malaise, 26 January 1966 ( 7 females);

19 February 1966 (1 female); 20 February 1966 ( 1 female); 22 March 1966 (11 females); 23 March 1966 (10 females); 24 March 1966 ( 5 females); 27 March 1966 ( 34 females); 3 April 1966 ( 19 females); near Maipu, $33^{\circ} 30^{\prime} \mathrm{S} 70^{\circ} 55^{\prime} \mathrm{W}, 510 \mathrm{~m}$, M.E Irwin, Malaise, 2 February 1966 ( 1 female); 12 February 1966 ( 7 females); 14 February 1966 ( 20 females); 21 February 1966 (2 females); 12 March 1966 (8 females); 16 March 1966 (18 females): 17 March 1966 ( 3 females); $550 \mathrm{~m}, 24$ March 1966 ( 24 females; 4 females, MNRJ); E.I. Schlinger, 14 January 1966 ( 1 female); El Canelo: $33^{\circ} 37^{\prime}$ S $71^{\circ} 35^{\prime}$ W, 950 m, E. I. Schlinger, 10 January 1966 ( 3 females); Lagunas: Magallanes, night, C.W. \& L. O’Brien, 13 January 1968 ( 1 female); Nuble: 40 km east of San Carlos, Ross and Michelbacher, 23 December 1950 (1 female); Aconcagua: Zapallar, Ross and Michelbacher, 15 December 1950 ( 1 female).

Notes.- The species was previously recorded only from Malleco (Soares and Carvalho 2005b).

## Palpibracus chilensis (Bigot, 1885)

Lectotype. - Male, deposited at Oxford University Museum of Natural History (Oxford, UK). Type-locality: Chile.

Diagnosis.- Palpus yellow; antennae dark brown, apex of pedicelum and base of flagellum yellow; frons brown; female with interfrontal setae; katepimeron ciliated; dorsum of mesonotum yellow with a median blackish brown vitta reaching the base of scutellum and almost reaching the dorsocentral row of setae (Fig. 4); anepisternum, anepimeron and almost the whole meron brown (Fig. 5); legs yellow with fore femur brown at middle and hind femur faint brown on apical third, in the male examined; male legs: fore coxa with apical spine; mid femur with a median depression on anterior surface; hind tibia bent with anteroventral and posteroventral fine setae as in Fig.56a (Malloch, 1934); abdomen blackish brown with grayish pollinosity (Fig. 6).

Color variation.- The two studied specimens show a brown lateral spot behind pronotum.
Material examined.- Chile: Malleco: 30 km W Angol, Nahuelbuta, $37^{\circ} 48^{\prime} \mathrm{S} 72^{\circ} 43^{\prime} \mathrm{W}$, 1060 m ., E.I. Schlinger, 13 February 1967 ( 1 male); Magallanes: 40 km W Laguna Amarga, $50^{\circ} 59^{\prime} \mathrm{S} 72^{\circ} 45^{\prime} \mathrm{W}$, M.E. Irwin and E.I. Schlinger, 7 December 1966 (1 female).

Notes.- A full redescription of this species, including illustrations of male and female terminalia, was published by Carvalho (1989a). The species was previously recorded from Curico and Malleco (Soares and Carvalho 2005b).

## Palpibracus confusus (Malloch, 1928)

Holotype.- Male, deposited at The Natural History Museum (London, UK). Type-locality: Argentina, Chubut, Valle del Lago Blanco.

Diagnosis.- Palpus brown; antennae dark brown, some specimens with apex of pedicelum and base of flagellum yellow; frons reddish brown; female without interfrontal setae; katepimeron ciliated; dorsum of mesonotum yellow with a median blackish brown vitta more or less as wide as the acrostichal row of setae and not reaching the base of scutellum; (Fig. 7); pleurae yellow, with inferior half of anepisternum and anepimeron shiny brown (Fig. 8); fore leg brown, with femorotibial joint yellow; mid and hind legs brown, with femora with basal third yellow; male legs: fore coxa with apical spine; mid femur with a marked depression on apical half of anterior surface; hind tibia bent with anteroventral and posteroventral rows of fine setae; abdomen blackish brown with grayish pollinosity (Fig. 9).

Color variation.- Malloch (1934) described the color of the palpus as "fuscous paler at base", but in Soares and Carvalho's (2005b) key, P. confusus appears to have yellow palpi. We consider the color as described by Malloch (1934), to be more accurate.

Material examined.- Chile: Nuble: 40 km east of San Carlos, Ross and Michelbacher, 23

December 1950 ( 1 male; 1 male MNRJ, 4 females; 1 female MNRJ); Cautin: 20 km east of Temuco, Ross and Michelbacher, 8 January 1951 ( 1 male); Santiago: El Canelo, $33^{\circ} 37^{\prime}$ S $71^{\circ} 35^{\prime}$ W, 950 m , EI. Schlinger, 10 January 1967 ( 1 female); Quebrada de la Plata, $33^{\circ} 30^{\prime} \mathrm{S} 70^{\circ} 55^{\prime}$ W, 550 m , M.E. Irwin, Malaise, 24 March 1966 ( 1 female); Fundo de la Montana Estero la Palma at Rio Temo, 6 km E Los Quenes, M.E. Irwin, 4 January 1967 (2 males).

Notes.-A full redescription of this species, including illustrations of male and female terminalia, was published by Carvalho (1989a). The species was previously recorded from several localities in Chile and Argentina (Soares and Carvalho 2005b); ours is the first record from Santiago.

## Palpibracus flavithorax Couri and Penny, sp. nov.

Holotype.- Male, deposited at CAS, labeled: "Chile: Magallanes: 4 km W Laguna Amarga, $50^{\circ} 59^{\prime} \mathrm{S} 72^{\circ} 45^{\prime}$ W, M.E. Irwin and E.I. Schlinger, 7 December 1966.

Diagnosis. - Palpus brown; antennae dark brown, with apex of pedicelum paler in some specimens; frons dark brown, reddish close to lunule; female without interfrontal setae; katepimeron bare; dorsum of mesonotum yellow without median vitta, a little gray pollinosity on acrostichal and dorsocentral rows of setae, more visible pre-suturally (Fig. 10); pleura with anepisternum, anepimeron and anterior and posterior spiracles yellow; katepisternum and meron brown (Fig. 11); legs brown ; male legs: fore coxa with a thin spine; mid femur with a depression on central part of anterior surface; row of long posteroventral setae, except on basal fourth; hind tibia slightly bent with anteroventral and posteroventral fine setae on middle third; abdomen brown with grayish pollinosity (Fig. 12).

The name of this species refers to the totally yellow dorsum of mesonotum with no traces of brown vitta.

Male.- Length. Body: 7.5-8.5 mm; wing 7.5-8.5 mm.
General coloration.- Frons dark brown, reddish closer to lunule; fronto orbital plate brown; gena reddish brown above and yellow below. Palpus brown. Antenna brown with apex of pedicelum paler; dorsum of mesonotum yellow with no median vitta, a little gray pollinosity on acrostichal and dorsocentral rows of setae, more visible pre-suturally (Fig. 10); pleura with anepisternum, anepimeron and anterior and posterior spiracles yellow; katepisternum and meron brown (Fig. 11). Calypters and haltere yellow. Wing hyaline. Legs brown. Abdomen blackish brown with grayish pollinosity (Fig. 12).

Head.- Holoptic; anterointernal facets developed. Frontal row with 8-9 pairs of setae. Vertical internal and external similar in length. Antenna inserted a little below the medium level of eyes; flagellum about twice the pedicelum length. Palpi falciform.

Thorax.- Dorsocentrals 2:4; acrostichals 3 pairs pre-suturally and one long post-sutural pair inserted at the same level as the fourth dorsocentral; postpronotals; 1 presutural; 2 intralars; 1 prealar; 2 supralars; 2 postsupralars. Notopleuron with two setae, the posterior shorter than the anterior. Scutellum with one faint pair of basal setae, 1 strong pair of sub-basal; 1 pair preapical lateral and 1 strong pair apical setae. Anepisternum with a series of $7-8$ strong setae; 3 thin setae on anterior angle. Katepisternals 1:3. Katepimeron bare. Inferior calypter about 1.6-1.8 the length of the superior. Wing vein $\mathrm{R}_{4+5}$ and $\mathrm{M}_{1+2}$ almost parallel to apex. Anterior coxa with a thin apical spine. Mid femur on anterior surface with a central depression, row of long posteroventral setae, except on basal fourth: posterior to posterodorsal surface with 4 preapical setae; mid tibia with 4-5 setae posterodorsals and posteroventrals; strong apical setae on anteroventral, ventral and dorsal surfaces; hind femur with 4-5 anteroventral setae on apical third; anterodorsal surface with a complete row of setae, fine on basal half and strong on apical; hind tibia slightly bent with 2-3 anterodorsal and posterodorsal sparse setae; anteroventral and posteroventral fine setae on middle third.

Tervinalia. - Sternite 5 as long as wide, with two long setae on each side, close to margin (Fig. 35). Cercal plate wider than long, surstili large (Fig. 36). Hypandrium and aedeagus as in Fig. 37-38.

Female.- Length. Body: 7.5-8.5 mm; wing: 7.5-8.5 mm. Differs from male as follows: interocular space about one third of head width; hind tibia not bent.

Ovipositor.- Tergites and sternites 6 and 7 thin, tergite 8 wider. Epiproct with short and strong spines (Figs 39-40). Spermatheca as in Fig. 41.

Other Material examined.- Paratypes labeled: Chle:: Magallanes: 4 km W Laguna Amarga, $51^{\circ} 00^{\prime}$ S $72^{\circ} 48^{\circ} \mathrm{W}$, Malaise, 300 m , E.I. Schlinger and M.E. Irwin 7 December $1966(1$ male, 1 male and 1 female, MNRJ); 8 December 1966 ( 1 male); Santiago: Quebrada de la Plata, $33^{\circ} 30^{\prime}$ S $70^{\circ} 55^{\prime} \mathrm{W}$, near Maipu, Malaise, 550 m , M.E. Irwin, 16 March 1966 ( 1 female); Rinconada, Maipu, $30^{\circ} 31^{\prime} \mathrm{S} 70^{\circ} 47^{\prime} \mathrm{W}$, Malaise, 550 m. M.E. Irwin, 22 March 1966 ( 1 female); 23 March 1966 ( 1 female); 27 March 1966 ( 2 females); 3 April 1966 (1 female). Bio Bio: El Abanico, Ross and Michelbacher, 30 December 1950 (1 male).

DISCUSSION.- P. flavithorax can be easily distinguished from its congeners by the dorsum of mesonotum being totally yellow, with no black vittae, and the spine on fore coxa being much thinner than in all other species in which this structure is present.

## Palpibracus nigriventris (Malloch, 1928)

Holotype.- Female, deposited at United States National Museum (Washington, USA). Type-locality: Chile.

Diagnosis.- Male with dorsal eye facets very enlarged; palpus and antenna dark brown; frons dark brown; female with interfrontal setae; katepimeron bare; dorsum of mesonotum yellow with a wide median blackish brown vitta, reaching the base of scutellum and extending to dorsocentral row of setae (Fig. 13); pleurae with anepisternum and anepimeron yellow and katepisternum and meron brown (Fig. 14); legs brown; male legs: fore coxa without apical spine; mid femur with no depression; 2 posteroventral straight and erect setae on basal half; hind tibia bent with an anteroventral row of fine setae and a posteroventral sub-median fine tuft of long setae (Fig. 50a, Malloch, 1934); abdomen shiny blackish brown with very little grayish pollinosity (Fig. 15).

Color variation.- The series examined does not show color variation.
Material examined. - Chle: Magallanes: 40 km W Laguna Amarga, $50^{\circ} 59^{\prime} \mathrm{S} 72^{\circ} 45^{\prime} \mathrm{W}$, M.E. Irwin and E.I. Schlinger, 7 December 1966 ( 3 males); Llanquihue: Petruhue, 100 m, Notofagus Forest, M.E. Irwin and E.I. Schlinger, 15 November 1966 ( 1 male; 1 male, MNRJ, and 3 females); $41^{\circ} 08^{\prime} \mathrm{S} 72^{\circ} 25^{\prime} \mathrm{W}$, 100 m, M.E. Irwin and E.I. Schlinger, Malaise, 15 November 1966 ( 1 male and 1 female); Malleco: Nahuelbuta National Park, 30 km W Angol, E.I. Schlinger, 12 February 1967 ( 1 male); Osorno: 8 km W la Picada, "El Refugio", Volcan Osorno, $41^{\circ} 04^{\prime} \mathrm{S} 72^{\circ} 26^{\prime}$ W, 350 m, E.I. Schlinger, 6 February 1967 ( 7 males; 1 male, MNRJ, and 10 females; 1 female, MNRJ); Puerto Varas, Ross and Michelbacher, 16 January 1951 (1 female); Tierra del Fuego: 35 km SW Cameron, 30 m , Notofagus Forest, M.E. Irwin, 2 December 1966 ( 1 female).

Notes.- A full redescription of this species, including illustrations of male and female terminalia, was published by Carvalho (1989a). The species was previously recorded from several localities in Chile and Argentina (Soares and Carvalho 2005b); ours are the first records from Osorno and Tierra del Fuego.

## Palpibracus peruvianus (Malloch, 1929)

Holotype.- Male, deposited at United States National Museum (Washington, USA). Typelocality: Chile, Perales.

Diagnosis.- Palpus yellow; antennae dark brown, some specimens with pedicel reddish brown; frons dark brown; female with interfrontal setae; katepimeron bare; dorsum of mesonotum
brown with grayish pollinosity with 4 shining dark vittae; postpronotum yellow; scutellum yellow on sides and with a median dark brown vitta (Fig. 16); pleurae dark brown with gray pollinosity (Fig. 17); legs brown; male legs: fore coxa without apical spine; mid femur without depression, 10-12 long and strong straight setae on basal half; hind tibia straight with fine, short and scattered fine posteroventral setae (Fig. 58c, Malloch, 1934, as angolensis); abdomen yellow with a brown median vitta on tergites $1+2-4$; tergites 3 and 4 with a triangular dark brown lateral spot; tergite 5 dark brown on basal third; tergites $3-5$ with gray pollinosity on basal third, in certain lights (Fig. 18); tergite 5 yellow in female (Fig. 19).

COlor variation. - The color of the abdomen, especially in males, can be a little darker than in females, with tergite 4 darker laterally.

Material examined.- Chile: Santiago: Quebrada de La Plata, $33^{\circ} 30^{\prime}$ S $70^{\circ} 55^{\prime}$ W, M.E. Irwin, 550 m, Malaise, 12 March 1966 ( 4 females); 16 March 1966 ( 4 females); 17 March 1966 ( 5 females, 1 female, MNRJ); 24 March 1966 ( 56 females); near Maipu, $510 \mathrm{~m}, 8$ February 1966 ( 1 female); 9 February 1966 (3 females); 10 February 1966 ( 1 female); 12 February 1966 ( 54 females); 21 February 1966 ( 1 female); 9 March 1966 ( 15 females); 12 March 1966 ( 8 females, 2 females, MNRJ); 16 March 1966 (3 females); 17 March 1966 ( 7 females); 23 March 1966 ( 4 females); 24 March 1966 ( 66 females), 17 October 1966 ( 1 male); Rinconada, Maipu, $33^{\circ} 31^{\prime} \mathrm{S} 70^{\circ} 47^{\prime}$ W, M.E. Irwin, 26 January 1966 ( 1 female); 550 m , Malaise, 22 March 1966 (42 females); 23 March 1966 ( 15 females); 24 March 1966 ( 1 female); 27 March 1966 ( 182 females); 3 April 1966 (2 females); 510m, 26 January 1966 ( 1 female); 23 March 1966 ( 11 females); 24 March 1966 ( 33 females); 27 March 1966 ( 39 females); 3 April 1966 ( 19 females); $33^{\circ} 34^{\prime} \mathrm{S} 71^{\circ} 14^{\prime} \mathrm{W}, 450 \mathrm{~m}$, Malaise-Corn, N. Hichins and M.E. Irwin, 17 March 1966 (2 females); $33^{\circ} 31^{\prime} \mathrm{S} 70^{\circ} 47^{\prime} \mathrm{W}$, 450 m , N. Hichins and M.E. Irwin, 1 April 1966 ( 1 female); 15 km east de Las Condes, $33^{\circ} 25^{\prime} \mathrm{S} 70^{\circ} 35^{\prime}$ W, M.E. Irwin, 19 March 1966 ( 1 female); Coquimbo: Fray Jorge National Park, 15 km SW Pachingo, 100-200 m, E.I. Schlinger and M.E. Irwin, 20 October 1966 ( 1 female); Hacienda Illapel. $600-900 \mathrm{~m}, 31^{\circ} 36^{\prime} \mathrm{S} 71^{\circ} 07^{\prime} \mathrm{W}$, Schlinger, Irwin and Peña, 19 October 1966 (2 males, female); Cautin: 2 km SE Villarica, 140 m , E.I. Schlinger and M.E. Irwin, 18 December 1966 (1 male; 1 male, MNRJ). Argentina: Neuquen: Martin de Los Andes, W.W. Middlekauff, 7 April 1980 ( 1 female).

Notes.- A full redescription of this species, including illustrations of male and female terminalia, was published by Carvalho (1989a). The species was previously recorded from Bio Bio, Curico, Malleco, and Perales in Chile and in Rio Negro in Argentina (Soares and Carvalho 2005b); all of our locality records (see Material examined above) are new.

## Palpibracus pilosus (Macquart, 1851)

Lectotype.- Male, deposited at Museum National d'Histoire Naturelle (Paris, France). Type-locality: Chile, Magellan Strait.

Diagnosis.- Palpus yellow; antennae with pedicel yellow and flagellum brown; katepimeron pilose; dorsum of mesonotum blackish with two gray pollinose vittae to dorsocentral row of setae; postpronotum, scutellum and lateral dorsum of mesonotum yellow post-suturally (Fig. 20); pleura brownish, concolorous with dorsum of mesonotum; katepisternum with dark yellow areas in some specimens (Fig. 21); legs brown, with fore femur, middle and hind third (except apex) of hind femur and basal half of hind tibia blackish brown; fore coxa with apical spine ( $2-3$ on each side); mid femur without depression; posteroventral surface with about 8 or more strong setae on basal third in an irregular series; hind femur bent: hind tibia strongly bent with long anteroventral and posteroventral fine setae on apical half; abdomen shiny black brown with grayish pollinosity (Fig. 22).

Material examined. - Chile: Tierra del Fuego: 35 km SW Cameron, 30 m , wet Notofagus Forest, E.I. Schlinger and M.E. Irwin. 2 December 1966 ( 13 males; 2 males. MNRJ); Magallanes: 4 km W Laguna Amarga, $50^{\circ} 59^{\prime}$ S $72^{\circ} 45^{\prime}$ W, M.E. Irwin and E.I. Schlinger, 7 December 1966 ( 1 female).

Notes.- A full redescription of this species, including illustrations of male and female terminalia. was published by Carvalho (1989a). Males are easily distinguished by the numerous ( 8 or
more) strong setae on basal third of posteroventral surface. The species has already been recorded from our localities (see Soares and Carvalho 2005b).

## Palpibracus schlingeri Couri and Penny, sp. nov.

Holotype.- Male, deposited at CAS, labeled: "Chile: Santiago:, Quebrada de la Plata, Near Maipu, $510 \mathrm{~m}, 33^{\circ} 30^{\prime} \mathrm{S} 70^{\circ} 55^{\prime} \mathrm{W}$, Malaise, M.E. Irwin, 2 February $1966 . "$

DiAgNosis. - Palpus brown; antennae dark brown, with apex of pedicelum yellow; frons dark brown, reddish orange close to lunule; female without interfrontal setae; katepimeron bare; dorsum of mesonotum shiny yellow with a median blackish brown vitta not reaching base of scutellum and not larger than the acrostichal row of setae (Fig. 23); pleura with anepisternum and anterior and posterior spiracles yellow; katepisternum and meron shiny black (Fig. 24); legs brown; male legs: fore coxa without apical spine; mid femur without depression; row of posteroventral setae sparse and stronger on apical two-thirds; hind tibia a little sinuous with anteroventral and posteroventral fine setae on middle third; abdomen shiny blackish brown with grayish pollinosity (Fig. 25).

Male.- Length. Body: $7-8 \mathrm{~mm}$; wing: $7.5-8 \mathrm{~mm}$.
General coloration.- Frons dark brown, reddish close to lunule; fronto orbital plate brown, silvery pollinose; gena and palpus brown. Antenna brown with apex of pedicel yellow. Dorsum of mesonotum shiny yellow with a median blackish brown vitta not reaching base of scutellum and not larger than the acrostichal row of setae (Fig. 23); postpronotum and scutellum yellow; pleura with anepisternum and anterior and posterior spiracles yellow; katepisternum and meron shiny black (Fig. 24). Calypters and haltere yellow. Wing hyaline. Legs brown. Abdomen brown with grayish pollinosity (Fig. 25).

Head.- Holoptic; anterointernal facets developed. Frontal row with 6 pairs of setae. Vertical internal and external short, similar in length. Antenna inserted at medium level of eyes; flagellum about twice the pedicelum length. Palpi falciform.

Thorax.- Dorsocentrals 2:4; acrostichals 2 pairs of pre-suturals and an irregular series of short setae post-suturally the last one as long as the dorsocentrals; 2 postpronotals; 1 presutural; 2 intralars; 1 prealar; 2 supralars; 2 postsupralars. Notopleuron with two setae, the posterior shorter than the anterior. Scutellum with one pair of basal fine setae, 1 strong sub-basal, 1 pre-apical fine and 1 strong apical. Anepisternum with a series of 7-8 strong setae; 2 thin setae on anterior angle. Katepisternals 1:2. Katepimeron bare. Inferior calypter about 1.8 the length of the superior. Wing vein R4+5 and M1 +2 parallel to apex. Anterior coxa without an apical spine. Mid femur with 4 preapical setae on posterior surface; row of posteroventral setae sparse, stronger on apical twothirds. Mid tibia on anterodorsal and posterodorsal surfaces with 4-5 setae; ventral posteroventral and ventral surfaces with an apical seta. Hind femur with a complete row of anterodorsal setae; anteroventral surface with 4-5 setae on apical third; dorsal and posterodorsal surfaces with preapical setae; anteroventral surface with a row of 5 setae on basal third and anterodorsal surface with a complete row of setae. Hind tibia a little sinuous with anteroventral and posteroventral fine setae on middle third; anterodorsal surface with 5 sparse setae, posterodorsal surface with two setae at the end of median third.

Terminalia. - Sternite 5 longer than wide, with 2-3 stronger setae close to margin (Fig. 42). Cercal plate with a deep incision on posterior margin, surstyli large (Fig. 43). Hypandrium and aedeagus as in Figs 44-46.

Female.- Length. Body: 7-8 mm, wing: 7.5-8 mm. Differs from male as follows: interocular space about one third of head width; hind tibia not sinuous and without the anteroventral and posteroventral fine setae on middle third.

Ovipositor.—Long, with tergites and sternites somewhat developed, tergite 8 wider; epiproct with thin setae (Figs 47-48).

Other Material examined.- Paratypes labeled: same label as holotype, 2 February 1966 (1 female); 8 February 1966 (1 female); 9 February 1966 ( 1 female); 12 February 1966 ( 1 female); 14 February 1966 ( 3 females); 12 March 1966 ( 1 female); 16 March 1966 ( 3 females; 1 female, MNRJ); 23 March 1966 ( 1 female, 1 female, MNRJ); 24 March 1966 ( 2 females); 3 April 1966 ( 1 female); 550 m ; 12 March 1966 ( 1 female); 24 March 1966 ( 1 female); Rinconada, Maipu, $30^{\circ} 31^{\prime}$ S $70^{\circ} 47^{\prime}$ W, 23 March 1966 ( 7 females); 27 March 1966 (7 females); 3 April 1966 ( 1 female).

Discussion.- P. schlingeri, new species, comes closest to couplet 13 in the Soares and Carvalho (2005b) key, but it can be distinguished by the median brown vitta not reaching the base of scutellum, the absence of the apical spine on male fore coxa, and the absence of the depression on the male mid femur.

## Palpibracus spicatus (Malloch, 1934)

Holotype.- Male, deposited at The Natural History Museum (London, UK). Type-locality: Chile, Casa Pangue.

Diagnosis.- Palpus brown; antennae dark brown, some specimens with apex of pedicelum and base of flagellum yellow; frons dark brown; female without interfrontal setae; katepimeron bare; dorsum of mesonotum yellow with a median blackish brown vitta reaching base of scutellum and only a little wider than the acrostichal row of setae; scutellum yellow; (Fig. 26); pleurae yellow, except katepimeron and meron brown (Fig. 27); legs brown; male legs: fore coxa with an apical spine; mid femur with a marked depression on central part of anterior surface; row of posteroventral setae long and fine basally and stronger on apical half; hind tibia slightly bent with anteroventral and posteroventral fine setae on apical two thirds (Fig.58a, Malloch, 1934); abdomen brown with little grayish pollinosity (Fig. 28).

Color variation.- In most specimens the median mesothoracic vitta is straight whereas in a few specimens it abruptly enlarges very close to the scutellum, almost extending to dorsocentral row of setae.

Material examined.- Chile: Santiago: Quebrada de La Plata, $33^{\circ} 31^{\prime}$ S $70^{\circ} 47^{\prime}$ W, M.E. Irwin, 510 m, Malaise. 26 January 1966 (1 female); 16 March 1966 ( 1 female); 19 February 1966 (4 females); 20 February 1966 ( 5 females): 23 March 1966 ( 26 females); 24 March 1966 ( 32 females); 27 March 1966 (42 females); 3 April 1966 ( 55 females): 550 m .22 March 1966 ( 4 females); 23 March 1966 ( 4 females); 27 March 1966 ( 32 females); N. Hichins O., 13 October 1966 ( 1 female); $33^{\circ} 30^{\prime} \mathrm{S} 70^{\circ} 55^{\prime} \mathrm{W}$, near Maipu, 510 m , Malaise, 12 February 1966 (3 females); 14 February 1966 ( 16 females): 21 February 1966 ( 29 females); 9 March 1966 (2 females); 12 March 1966 ( 17 females, 1 female. MNRJ); 16 March 1966 ( 21 females; 2 females, MNRJ); 17 March 1966 ( 5 females); 23 March 1966 ( 6 females); 24 March 1966 ( 34 females); $550 \mathrm{~m}, 12$ February 1966 ( 1 female): 16 March 1966 ( 4 females): 17 March 1966 ( 2 females); 24 March 1966 ( 5 females; 1 female, MNRJ); $33^{\circ} 30^{\prime}$ S $70^{\circ} 50^{\prime}$ W. 510 m .2 February 1966 ( 4 females); 10 February 1966 ( 1 female); 12 February 1966 (2 females); 14 February 1966 (2 females); 9 March 1966 ( 7 females); 12 March 1966 ( 14 females); 14 March 1966 ( 1 female): 16 March 1966 ( 15 females): El Canelo. $33^{\circ} 35^{\prime}$ S $70^{\circ} 27^{\prime}$ W, 9 January 1967, M.E. Irwin (1 female): Llanquihue: NW Shore of Lago Chapo, E.I. Schlinger and M.E. Irwin, 13 November ( 1 male); Osorno: 30 km W of Purranque, Ross and Michelbacher, 16 January, 1951 ( 1 male); Curico: Fundo la Montana. Estero la Plama at Rio Teno, 6 km E Los Quenes, M. E. Irwin, 4 January 1967 ( 1 female).

Notes.- A full redescription of this species, including illustrations of male and female terminalia. was published by Carvalho (1989a). Llanquihue is a new geographic record for this species.

## Palpibracus trivittatus (Malloch, 1934)

Holotype.- Male, deposited at The Natural History Museum (London, UK). Type-locality: Argentina, Lake Correontoso.

Diagnosis. - Palpus brown; antennae dark brown, some specimens with apex of pedicelum and base of flagellum yellow; frons dark brown, reddish to lunule; female with interfrontal setae; katepimeron bare; dorsum of mesonotum yellow with three blackish brown vitta, sometimes fused in part, only the median reaches base of scutellum in some specimens; scutellum yellow (Fig. 29); pleurae yellow, except katepimeron and meron brown (Fig. 30); legs brown; male legs: fore coxa without an apical spine; mid femur without depression; with fine anteroventral and posteroventral row of setae; hind tibia almost straight with three or more anterodorsal and posterodorsal setae; row of anteroventral and posteroventral fine setae on basal half (Fig. 58b, Malloch, 19234); abdomen brown with little grayish pollinosity (Fig. 31).

Color variation.- Four females were examined and the vittae on mesonotum are not fused in one specimen and differently fused in the other three.

Material examined. - Chile: Malleco: Parque Nacional Nahuelbuta, P.C. Huchison, 8 January 1952 ( 1 female); Nuble: $2-7 \mathrm{~km}$ (no direction given on label) Las Trancas, Malaise, E.I. Schlinger, 29 January 1967 ( 1 female); Valdivia: 24 km S Valdivia, E.I. Schlinger, 3 February 1967 ( 1 female, MNRJ); Cautin: 12,3 km N Loncoche, 280 m , E.I. Schlinger and M.E. Irwin, 18 December 1966 ( 1 female).

Notes.- A full redescription of this species with illustrations of male and female terminalia is found in Carvalho (1989a). No males examined. The male characters on diagnoses are from Malloch (1934) and Carvalho (1989a). Nuble, Valdivia, and Cautin are new geographical records for this species.

## Palpibracus vittatus Couri and Penny, sp. nov.

Holotype. - Male, deposited at CAS, labeled: "Chile: Cautin: 20 km E of Temuco, Ross and Michel/bacher, 8 January 1951."

Diagnosis.- Palpus and antennae brown; frons dark brown; female without interfrontal setae; katepimeron bare; dorsum of mesonotum shiny yellow with a median blackish brown vitta between acrostichal row of setae pre-suturally, becoming wider post-suturally reaching the dorsocentral row of setae and reaching base of scutellum (Fig. 32); pleura with anepisternum and anepimeron yellow; katepisternum and meron shiny brown (Fig. 33); legs brown; male legs: fore coxa with a strong apical spine; mid femur with a marked depression on central part of anterior surface, with a group of short, strong and curved setae on its apex; posteroventral surface with long and strong setae on apical third; hind tibia bent with a complete row of fine anteroventral setae, posteroventral surface with a group of setae with curved apex on apical third, but not reaching the apex of the leg; abdomen shiny blackish with grayish pollinosity (Fig. 34).

The name of this species is derived from the Latin vitta, in reference to the unsual shape of the median vitta on the dorsum of the mesothorax.

Male.- Length. Body: 7.8 mm ; wing: 8 mm
General coloration.- Frons dark brown; fronto orbital plate brown; gena brown in male and dark yellow in female. Palpus and antenna brown. Postpronotum and scutellum yellow; dorsum of mesonotum shiny yellow with a median blackish brown vitta between acrostichal row of setae, becoming wider post-suturally reaching the dorsocentral row of setae and base of scutellum (Fig. 32); pleura with anepisternum and anepimeron yellow; katepisternum and meron shiny brown (Fig. 33); calypters and haltere yellow. Wing hyaline. Legs brown. Abdomen shiny brown with grayish pollinosity (Fig. 34).

Head.- Holoptic; antero-internal facets developed. Frontal row with 6 pair of setae. Vertical internal and external setae short and similar in length. Antenna inserted at middle of eye; flagellum about twice the pedicelum length. Palpi falciform.

Thorax.- Dorsocentrals 2:4; acrostichals: 2 pair of presuturals and irregular series of short setae post-suturally, the last one as long as the dorsocentral; 2 postpronotals; 1 presutural; 2 intralars; 1 prealar; 2 supralars; 2 postsupralars. Notopleuron with two setae, the posterior shorter than the anterior. Scutellum with one pair of basal setae, 1 strong sub-basal, 1 pre-apical and 1 strong apical. Anepisternum with a series of 6-7 strong setae; 2 thin setae on anterior angle. Katepisternals 1:2. Katepimeron bare. Inferior calypter about 1.8 the length of the superior. Wing vein $\mathrm{R}_{4+5}$ and $\mathrm{M}_{1+2}$ a little divergent to apex. Anterior coxa with a strong apical spine. Male mid femur with a marked depression on central part of anterior surface, with a group of short, strong and curved setae on its apex; anteroventral and posteroventral surfaces with long and strong setae on apical third; posteroventral surface with 4 strong setae on basal third; 3 preapical setae on dorsal to posterodorsal surfaces. Mid tibia with 3 ventral setae on middle third; posteroventral surface with 4 sparse setae on apical two/thirds. Hind femur with a complete anterodorsal row of setae; anteroventral surface with setae on apical third; hind tibia bent with a complete row of fine anteroventral setae, posteroventral surface with a group of setae with curved tip on apical third, but not reaching the apex; anterodorsal surface with a row of sparse setae stronger closer to apex.

Terminalla.- Sternite 5 a little longer than wide, except in middle (Fig. 49). Cercal plate with a deep anterior incision, surstili large (Fig. 50). Hypandrium and aedeagus as in Figs 51-52.

Female.- Length. 7.8 mm , wing: 8 mm . Differs from male as follows: interocular space about one third of head width; fore coxa with no spines; mid femur without the sexual secondary characters; hind tibia not bent and with 3 anterodorsal setae; 2 posterodorsals inserted at the limits of each third and 2 anteroventrals on middle third.

Ovipositor.-General shape a little thinner than in other species and with cerci very short (Figs 53-54).

Other Material examined.- Paratype labeled: Chile: Santiago: Quebrada de la Plata Fundo, Rinconada, Maipu, $33^{\circ} 31^{\prime} \mathrm{S} 70^{\circ} 47^{\prime}$ W, 510 m, M.E. Irwin, 26 January 1966 ( 1 female).

Discussion.- Although P. vittatus comes out at couplet 11 in Soares and Carvalho's (2005b) key, it can be easily distinguished from its congeners by the peculiar median stripe on mesonotum that enlarges post-suturally, reaching the dorsocentral row of setae.

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## Literature Cited

Albu'querque. D. De O. 1951. Quinta nota sobre os tipos de Macquart (Diptera-Muscidae), existentes no Museu Nacional de História Natural de Paris e descrição de uma espécie nova, proveniente do Chile. Boletim do Museu Nacional do Rio de Janeiro (Zoologia) 105:1-17.
C.arvalho, C.J.B. De. 1989a. Revisão das espécies e posição sistemática de Palpibracus Rondani (Diptera,

Muscidae). Revista Brasileira de Zoologia 6:325-375.
Carvalho, C.J.B. De. 1989b. Classificação de Muscidae (Diptera): uma proposta através da análise cladística. Revista Brasileira de Zoologia 6:627-648.
Carvalho, C.J.B. de, and M.S. Couri. 2002. Part I. Basal groups. Pages 17-132 in C.J.B. de Carvalho, ed., Muscidae (Diptera) of the Neotropical Region: Taxonomy. Curitiba, Editora Universidade Federal do Paraná.
Carvalho, C.J.B. de; M.S. Couri; A.C. Pont; D. Pamplona and S.M. Lopes. 2005. A Catalogue of the Muscidae (Diptera) of the Neotropical Region. Zootaxa 860:1-282.
Lopes, S.M., and A. Khouri. 1996. Descrição de uma espécie nova de Palpibracus Rondani, 1863 do Chile (Diptera, Muscidae, Azelinae, Reiwardtiini). Ceres 43:454-458.
Malloch, J.R. 1934. Muscidae. In: Diptera de Patagonia e South Chile 7:171-346.
Pamplona, D.M., and M.S. Couri. 2000. Espécie nova de Palpibracus Rondani (Diptera, Muscidae, Azelinae, Reiwardtiini). Boletim do Museu Nacional, Nova Série, Zoologia 431:1-4.
Rondani, C. 1864. Dipterorum species et genera aliqua exotica revisa et annotate novis nonnulis descriptis. Achivio per la Zoologia, l"Anatomia e la Fisiologia 3:1-99.
Soares, E.D.G., and C.J.B. de Carvalho. 2004. A new combination in Brachygasterina Macquart (Diptera, Muscidae). Revista Brasileira de Entomologia 48:431.
Soares, E.D.G., and C.J.B. de Carvalho. 2005a. Biogeography of Palpibracus Rondani (Diptera: Muscidae): an integrative study using panbiogeography, parsimony analysis of endemicity, and component analysis. Pages 485-494 in J. Llorente Bousquets and J.J. Morrone, eds., Regionalización biogeográfíca en Iberoamérica y tópicos afines. Faculdad de Ciencias, UNAM, Mexico.
Soares, E.D.G., and C.J.B. de Carvalho. 2005b. Taxonomia, análise cladística e descrição de uma espécie nova de Palpibracus Rondani (Diptera, Muscidae). Revista Brasileira de Entomologia 49: 171-180.

Figure 1. Palpiracus canvalhoi Lopes and Khouri, 1996; dorsum of mesothorax
Figure 2. Palpiracus carvalhoi Lopes and Khouri, 1996; pleurae
Figure 3. Palpiracus carvalhoi Lopes and Khouri, 1996; dorsum of abdomen
Figure 4. Palpibracus chilensis (Bigot,1885); dorsum of mesothorax
Figure 5. Palpibracus chilensis (Bigot,1885); pleurae
Figure 6. Palpibracus chilensis (Bigot.1885); dorsum of abdomen
Figure 7. Palpibracus confusus (Malloch, 1928); dorsum of mesothorax
Figure 8. Palpibracus confiusus (Malloch, 1928); pleurae
Figure 9. Palpibracus confusus (Malloch, 1928); dorsum of abdomen
Figure 10. Palpibracus flavithorax Couri and Penny, new species; dorsum of mesothorax
Figure 11. Palpibracus flarithorax Couri and Penny, new species; pleurae
Figure 12. Palpibracus flavithorax Couri and Penny, new species; dorsum of abdomen
Figure 13. Palpibracus nigriventris (Malloch, 1928): dorsum of mesothorax
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Figure 17. Palpibracus pertwianus (Malloch, 1929); pleurae
Figure 18. Palpibracus perwvianus (Malloch, 1929); dorsum of abdomen, male
Figure 19. Palpibracus pernvianus (Malloch, 1929); dorsum of abdomen, female


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Figure 35. Palpibracus flavithorax Couri and Penny, new species; male, sternite 5
Figure 36. Palpibracus flavithorax Couri and Penny, new species; male, cercal plate and surstily, dorsal view Figure 37. Palpibracus flavithorax Couri and Penny, new species; male, hypandrium
Figure 38. Palpibracus flavithorax Couri and Penny, new species; male, aedeagus, lateral view Figure 39. Palpibracus flavithorax Couri and Penny, new species; female, ovipositor, dorsal view Figure 40. Palpibracus flavithorax Couri and Penny, new species; female, ovipositor, ventral view Figure 41. Palpibracus flavithorax Couri and Penny, new species; female, spermathecae


Figure 42. Palpibracus schlingeri Couri and Penny, new species; male, sternite 5
Figure 43. Palpibracus schlingeri Couri and Penny, new species; male, cercal plate and surstily, dorsal view
Figure 44. Palpibracus schlingeri Couri and Penny. new species: male, hypandrium
Figure 45. Palpibracus schlingeri Couri and Penny, new species: male, aedeagus, dorsal view
Figure 46. Palpibracus schlingeri Couri and Penny. new species; male, aedeagus, lateral view
Figure 47. Palpibracus schlingeri Couri and Penny, new species; female, ovipositor, dorsal view
Figure 48. Palpibracus schlingeri Couri and Penny, new species; female, ovipositor, ventral view


Figure 49. Palpibracus vittatus Couri and Penny, new species; male, sternite 5
Figure 50. Palpibracus vittatus Couri and Penny, new species; male, cercal plate and surstily, dorsal view Figure 51. Palpibracus vittatus Couri and Penny, new species; male, hypandrium
Figure 52. Palpibracus vittatus Couri and Penny, new species; male, aedeagus, lateral view
Figure 53. Palpibracus vittatus Couri and Penny. new species; female, ovipositor, dorsal view
Figure 54. Palpibracus vittatus Couri and Penny, new species; female, ovipositor, ventral view


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## PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES Fourth Series

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# Eggs of Stylogaster Macquart (Diptera: Conopidae) on Madagascan Muscids (Diptera: Muscidae) 

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#### Abstract

The genus Stylogaster Macquart (Diptera, Conopidae) is represented by five species in Madagascar. All of the species are known to oviposit their dart-like eggs on cockroaches and calyptrate Diptera. Seven genera of Muscidae have previously been recorded as hosts, including two unnamed species of Dichaetomyia from Madagascar. The present paper records seven additional Madagascan muscid hosts: Deltotus facetus Seguy, Deltotus viola Zielke, Dichaetomyia apicalis (Zielke), Dichaetomyia basialaris (Zielke), Dichaetomyia tristis (Zielke), Neomyia setulosa (Zielke), and Phaonia, sp. nov. The records for Deltotus and Neomyia are the first for these genera. A brief discussion of their associations is given.


During a study of the muscid flies from Madagascar collected by the "Madagascar Arthropod Biodiversity Project," a program developed by the California Academy of Sciences (Couri et al., in prep.), eggs of Stylogaster Macquart (Diptera, Conopidae) were observed on some specimens.

The genus Stylogaster occurs in North and South America, Africa south of the Sahara, Madagascar, parts of Asia, the Philippines, and New Guinea (Smith 1967). Fourteen species are known from the Afrotropical region, five of them occurring in Madagascar - $S$. camrasi Stuckenberg, 1963; S. malgachensis Camras, 1962; S. pauliani Camras, 1962; S. seguyi Camras, 1962 and S. seyrigi Séguy, 1932 (Smith 1980).

The larvae of Stylogaster species are parasites on cockroaches and calyptrate Diptera, and the females are often seen hovering over the heads of marching columns of army ants (Hymenoptera: Dorylinae) and darting after their hosts, which are fleeing from the ant columns (Smith and Peterson 1987). Because of its remarkable biology and morphology, the genus is placed in its own subfamily, the Stylogastrinae.

Stuckenberg (1963) recorded Stylogaster eggs on some Muscidae species in southern Africa: Dichaetomyia serena (Stein), Dichaetomyia sp. nov., Dichaetomyia quadrata (Wiedemann), Dimorphia setulosa (Stein), Dimorphia tristis (Wiedemann) and Pyrellina marsya (Walker) (as $P$. chrysotelus [Walker]). In that publication, he pointed out that these species were all similar in appearance (Dichaetomyia-shape) and all were pale brownish or yellowish-brown in colour, except $P$. marsya, which is a dark-blue species with tergite V yellow.

Smith (1967) mentioned two unnamed species of Dichaetomyia from Madagascar impaled with Stylogaster eggs. In 1969, Smith added new records of adult muscids with Stylogaster eggs belonging to the genera Helina Robineau-Desvoidy, Haematobosca Bezzi (as Bdellia Enderlein), Phaonia Robineau-Desvoidy, and Stomoxys Geoffroy, and he also discussed their association with ants or mammalian dung (Smith 1969).

Lopes (1937) first noted the distinctive species-level characters of some of the Stylogaster dartlike eggs, and Smith (1967) gave a key for the identification of the Afrotropical (and Malagasy) species of Stylogaster, based on the morphology of the egg.

Except for the egg, the life-histories of species in this genus are litle known. The morphology of the larvae is restricted to a first instar larva extracted from an egg found in Calodexia (Diptera, Tachinidae), and what may have been a second instar larva in a cockroach, both described by Rettenmeyer (1961).

What little else is known of the biology of Stylogaster was also reviewed by Rettenmeyer (1961), the early literature by Smith (1966), and more recent knowledge of the biology and taxonomy by Smith (1967).

The aim of this paper is to record the new data obtained on the Madagascan muscid hosts of Stylogaster and to present a brief discussion on this association.

## Materials and Methods

The materials studied are in the entomological collections of the California Academy of Sciences (CAS, San Francisco, California, USA).

The colour photos were made using Syncroscopy/JVC Auto-Montage with a Leica M 420 optical microscope.

## Results and Discussion

About 1800 muscid specimens from Madagascar were examined and eleven of them (approximately $0.7 \%$ ), belonging to seven species, were found to be impaled with Stylogaster eggs:

Deltotus facetus Seguy. 1935: Madagascar: Fianarantsoa Province: Ranomafana National Park, Vohiparara, at broken bridge, elev: $1100 \mathrm{~m}: 21^{\circ} 13.57^{\prime} \mathrm{S} 47^{\circ} 22.19^{\prime} \mathrm{E}$, malaise trap, in high altitude rainforest; 31 March-8 April 2002, collection code MA-02-09A-23, 1 male. CASENT 3010583: 26-31 March 2002, R. Harin'Hala, collection code MA-02-09A-22. 1 male. CASENT 3009402; Belle Vue at Talatakely, elev. 1020 m. $21^{\circ} 15.99^{\prime} \mathrm{S} 47^{\circ} 25.21^{\prime} \mathrm{E}$. malaise trap. secondary tropical forest. 12-19 February 2002. R. Harin'Hala, collection code MA-02-09C-16, 1 female, CASENT 3009764.

Deltotus viola Zielke, 1972: Madagascar: Fianarantsoa Province: Ranomafana National Park, Vohiparara, at broken bridge. elev. $1110 \mathrm{~m} ; 21^{\circ} 13^{\prime} 57^{\prime \prime} \mathrm{S} 47^{\circ} 22^{\prime} 19^{\prime \prime} \mathrm{E}$, malaise trap, in high altitude rainforest, 31 March-8 April 2002, R. Harin'Hala, collection code MA-02-09A-23, 1 female, CASENT 3010581; 1 female, CASENT 3010584.

Dichaetomvia apicalis (Zielke. 1972): Madagascar: Fianarantsoa Province: Ranomafana National Park. Vohiapara, at broken bridge, elev: $1100 \mathrm{~m}: 21^{\circ} 13^{\prime} 57^{\prime \prime} \mathrm{S} 47^{\circ} 22^{\prime} 19^{\prime \prime} \mathrm{E}$, malaise trap, in high altitude rainforest, 14-26 June 2002, collection code MA-02-09A-32, 1 female, CASENT 3010318.

Dichaetomyia basialaris (Zielke, 1972): Madagascar: Fianarantsoa Province: Ranomafana National Park. Belle Vue at Talatakely, elev: $1020 \mathrm{~m}: 21^{\circ} 15.99^{\prime} \mathrm{S} 47^{\circ} 25.21^{\prime} \mathrm{E}$. malaise trap, secondary tropical forest, 14-21 January 2002, R. Harin'Hala, collection code: MA-02-09C-12, 1 male, CASENT 3009843.

Dichaetomyia tristis (Zielke, 1972): Madagascar: Toliara Province: Andohahela National Park, Col du Sedro. $3.8 \mathrm{~km} 113^{\circ}$ ESE Mahamavo. $37.6 \mathrm{~km} 341^{\circ}$ NNW Tolagnaro; $24^{\circ} 45^{\prime} 50^{\prime \prime} \mathrm{S} 46^{\circ} 45^{\prime} 6^{\prime \prime}$ E, pitfall trap montane rainforest, elev: $900 \mathrm{~m}, 21$-25 January 2002, Fisher, Griswold et al., collection code: BLF5013, 1 female. CASENT 3009365. Fianarantsoa Province: Ranomafana National Park, Radio tower at forest edge, elev. $1130 \mathrm{~m} ; 21^{\circ} 15^{\prime} 05^{\prime \prime} \mathrm{S} 47^{\circ} 24^{\prime} 43^{\prime \prime} \mathrm{E}$, malaise trap, mixed tropical forest, 15-21 December 2001, R. Harin Hala, collection code: MA-02-09B-07. 1 male. CASENT 3010857.

Neomitia setulosa (Zielke, 1972): Madagascar: Antsiranana Province: Marojejy National Park, Manantenina River, $28.0 \mathrm{~km} 38^{\circ}$ NE Andapa. $8.2 \mathrm{~km} 333^{\circ}$ NNW Manantenina, elev. $450 \mathrm{~m} ; 14^{\circ} 26^{\prime} 12^{\prime \prime} \mathrm{S}$ $49^{\circ}+6^{\prime} 30^{\prime \prime}$ E, malaise trap - rain forest. 12-15 November 2003, B.L. Fisher et al., collection code BLF8723, 1 female. CASENT 3009084.

Phaonia sp. nov. Madagascar: Fianarantsoa Province: Ranomafana National Park, Belle Vue at Talatakely, elev. $1020 \mathrm{~m} ; 21^{\circ} 15^{\prime} 99^{\prime \prime} \mathrm{S} 47^{\circ} 25^{\prime} 21^{\prime \prime} \mathrm{E}$, malaise trap, secondary tropical forest, 12-19 February 2002. R. Harin'Hala, collection code: MA-02-09C-16, 1 male, CASENT 3009762.

Table 1 summarizes the host, sex, site and number of eggs.
All these species are new muscid host records for Stylogaster. Deltotus Séguy, which is endemic to Madagascar, and Neomyia Walker are new genus records.

Speculation on the association between the muscid flies, Stylogaster, and army ants has been made in the literature, but as the ant subfamily Dorylinae is entirely absent from some parts of Africa and from Madagascar, it is clear that at least some species of Stylogaster have no obligatory association with these ants (Stuckenberg 1963).

Table 1: Madagascan muscid flies with eggs of Stylogaster

| Host species | Sex | Site of egg | Number of eggs |
| :--- | :--- | :--- | :--- |
| Deltotus facetus Séguy | male | scutellum | 1 |
|  | female | mesonotum (presuturally) <br> tergite 5 | 1 |
|  | male | mesonotum (postsuturally) | 1 |
|  |  | eye | 1 |
| Deltotus viola Zielke | female | postpronotum | 1 |
|  |  | eye | 1 |
|  |  | female | notopleuron |
| Dichaetomyia | $1+2$ | 1 |  |
| Dichaetomyia basialaris (Zielke) | female | male | eye |
| Dichaetomyia tristis (Zielke) | female | mesonotum (presuturally) | 1 |
|  | male | mesonotum (postsuturally) | 1 |
| Neomyia setulosa (Zielke) | female | mesonotum (presuturally) | 1 |
| Phaonia sp. nov. |  | notopleuron | 1 |
|  | male | eye | 1 |
|  |  |  | 1 |

Stuckenberg (ibid.) pointed out that most of his records of muscids impaled with eggs were of species that are attracted to faeces, such as Dimorphia Malloch, and that all his recorded specimens were females. Thus, he suggested that Stylogaster species might search for their hosts in the vicinity of dung, where female muscids, less active at oviposition sites, would be easier prey. Stuckenberg recorded 19 specimens, all females and all from Southern Africa, impaled with Stylogaster eggs. Smith (1967) called attention to the fact that not all Dichaetomyia larvae are coprophagous, and in his study both sexes were about equally attacked. In a subsequent paper, Smith (1969) listed 23 specimens impaled with eggs, 20 females and 3 males. The sex ratio in the present study was 50:50.

Of the genera recorded here, Skidmore (1985) stated that Dichaetomyia species are strongly attracted to dung, and there are many records in the literature of these flies visiting excrement (human faeces, bovine, horse or goat dung). For instance, Neomyia breed mainly or exclusively in bovine dung, whereas Phaonia develops mainly in mosses and humus soil, rarely utilizing dung as a larval pabulum. Nothing is known about the life-history of Deltotus, but its systematic position among the metallic green/blue Muscini suggests that it, too, has coprophagous larvae.

In analyzing what attracts Malagasy Stylogaster to deposit eggs on host muscids, we examined large series of Dichaetomyia spp., Helina lucida (Stein), and Stomoxys. None were found to have

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Figures A-D (left). (A) Phaonia sp. n., male, head, 3/4 view. (B) Deltotus facetus Séguy, female, head and part of mesonotum, lateral view. (C) Deltotus viola Zielke, female, abdomen, lateral view. (D) Deltotus facetus Séguy, female, abdomen, lateral view

Stylogaster eggs. Helina lucida have coprophagous larvae whereas Dichaetomyia ssp. and Stomyxys do not. Although Stuckenberg (1963) suggested that the pale coloration of South African Dichaetomyia might be attracting Stylogaster for oviposition, the pale coloration of Malagasy Dichaetomyia ssp. and dark coloration of Helina lucida and Stomoxys appeared to have no effect on oviposition rates.

The maximum number of eggs per specimen recorded here was three. However, Stuckenberg (1963) recorded a maximum of four and Smith (1967) five.

In his discussion of the presence of the eggs on muscids, Stuckenberg (1963) wondered whether the muscids are the hosts themselves or whether they are carriers of the eggs to their true hosts.

Rettenmeyer (1961) suggested that the abundant muscid flies found over ant swarms in Panamá could be attracted to the noise, odour, or appearance of other flies flying over the ant swarms, rather than to the ants themselves. He also mentioned that other muscid species, which are attracted to the swarms, breed in the remains of booty deposited by the ants outside their nests.

Much more field study and collecting should be done to elucidate the associations among Stylogaster, muscids, and ants, and to discover the life-history of Stylogaster itself. Eggs of Stylogaster have been also recorded from other calyptrate Diptera found over raiding columns of army ants, such as Calodexia and Androeuryops (Tachinidae) in Panamá (Rettenmeyer 1961).

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## Literature Cited

Couri, M.S.; A.C. Pont, and N.D. Penny. (In prep.) Muscidae (Diptera) from Madagascar: Keys to identification, descriptions of new species, and new records.
Lopes, H. De Souza. 1937. Contribuição ao conhecimento do gênero Stylogaster. Arquivos do Instituto de Biologia Vegetal, Rio de Janeiro 3:257-293.
Rettenmeyer, C.W. 1961. Observations on the biology and taxonomy of flies found over swarm raids of army ants (Diptera: Tachinidae, Conopidae). University of Kansas Science Bulletin 42:993-1066.
Skidmore, P. 1985. The biology of the Muscidae of the world. Series Entomologica 29:1-550.
Smith, K.G.V. 1966. The larva of Thecophora occidensis, with comments upon the biology of Conopidae (Diptera). Journal of Zoology 149:263-276
S.ith, K.G.V. 1967. The biology and taxonomy of the genus Stylogaster Macquart, 1835 (Diptera: Conopidae, Stylogasterinae) in the Ethiopian and Malagasy regions. Transactions of the Royal Entomological Society of London 199:47-69.
S.irth, K.G.V. 1969. Further data on the oviposition by the genus Stylogaster Macquart (Diptera: Conopidae, Stylogasterinae) upon adult calyptrate Diptera associated with ants and animal dung. Proceedings of the

Royal Entomological Society of London, ser. A, 44:439-446.
Smith, K.G.V. 1980. Family Conopidae. Pages 511-517 in R.W. Crosskey, ed., Catalogue of the Diptera of the Afrotropical Region. British Museum (Natural History), London, UK.
Smith, K.G.V. and B.V. Peterson. 1987. Conopidae. Pages 749-756 in J.F. McAlpine, B.V. Peterson; G.E. Shewell; H.J. Teskey; J.R. Vockeroth and D.M. Wood, eds., Manual of Nearctic Diptera, vol. 2. Research Branch, Agriculture Canada, Monograph No.28. 1332 pp.
Stuckenberg, B.R. 1963. A study on the biology of the genus Stylogaster, with the description of a new species from Madagascar. Revue de Zoologie et Botaniques Africaines 68:251-275.

# PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES Fourth Series 

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# White Shark Attacks Upon Humans in California and Oregon, 1993-2003 

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#### Abstract

We report on 20 confirmed and five purported but unreliable incidents of unprovoked attacks by white sharks on humans in California and Oregon between 1993 and 2003. All attacks involved white sharks (Carcharodon carcharias). The discussion, map, and tables from McCosker and Lea's (1996) report are updated. The majority of attacks occurred at or near the surface, near shore, and often in the vicinity of pinniped colonies and/or river mouths and harbors. Attacks have now occurred during all months, and on surfers, breathhold and scuba divers, swimmers, hookah divers, kayakers, and, for the first time, on bodyboarders, a windsurfer, and a scuba diver using an electric propulsion device. Typical attack scenarios suggest that an adult $C$. carcharias mistakes its victim for a pinniped, its normal prey. Shark attacks were fewer during the extreme 1997-1998 ENSO (EI Niño/Southern Oscillation) oceanographic warming event. The defensive activity of humans after being attacked and its effect are discussed. We also comment on recent legislation concerning white shark protection and disallowing the attraction of white sharks by chumming.


In 1996, we (McCosker and Lea, 1996) reviewed the history, human activity, and shark activity involved with unprovoked attacks by white sharks (Carcharodon carcharias) upon humans in the eastern North Pacific Ocean (ENP). The last attack that we reported up ... it hat involving Rosemary Johnson on 10 October 1993. We begin this study with an attack that occurred so late in 1993 that we were unable to include it in our earlier paper. In the subsequent decade 20 unprovoked attacks upon humans by white sharks have occurred in the ENP. We herein report upon those attacks and update our analysis and conclusions.

The following is a brief review of literature concerning attacks by white sharks in the ENP. A more extensive listing occurs in our 1996 report, and a nearly complete bibliography of C. carcharias can be found in the edited volume that included it (Klimley and Ainley 1996). In California, nearly all unprovoked shark attacks on humans involve white sharks, particularly north of Point Conception ( $34^{\circ} 27^{\prime}$ N lat.) (Fig. 1). All known shark attacks in California between 1926 and 1979 were reviewed by Miller and Collier (1981). Subsequently, Lea and Miller (1985) added records for California and Oregon between 1980 and 1984, and Collier (1992) provided additional descriptions of attacks. More recently, Collier (2003) published a detailed account, with numerous photographs, of all known $20^{\text {th }}$ Century shark attacks in the eastern North Pacific. Egaña and McCosker (1984) described white shark attacks in Chile, comparing the similarities and differences to those in the eastern North Pacific. Ellis and McCosker (1991) listed eastern Pacific white shark attacks between 1926-1991 and described several in detail. And, as stated above, McCosker and Lea (1996) reviewed all eastern Pacific attacks until the end of October, 1993. We have been advised by Mrs.

[^3]W.C. Thompson (in litt.) of the following corrections that need be made to that report: the attack on Kenneth Gray (p. 423) occurred on 19 July 1971, not 1972; and the attack on Ken Kelton (p. 429) in 1992 occurred as he approached Steele (not Steel) Reef.

Several papers concerning white shark behavior that are relevant to this study have been published during the last decade; we will briefly describe those studies. Klimley et al. (2001) observed the pinniped-hunting strategy of white sharks at Año Nuevo Island in central California. They attached ultrasonic transmitters to seven adult white sharks during October and November and found: (a) the sharks spent a mean time of $39.5 \%$ of each day patrolling; (b) none moved far from a limited area; (c) the sharks spent equal amounts of activity in the same area during day and night; (d) the movements of the sharks relative to the island rookery were most often parallel to shore; and (e) some sharks preferentially patrolled but did not defend certain areas. In a study of white shark prey search behavior at Southeast Farallon Island (SFI) in north central California. Goldman and Anderson (1999) found that when searching for northern elephant seals (Mirounga angustirostris), the sharks combine alongshore and onshore/offshore movements while swimming close to the bottom until the depth reaches 30 m , thereby allowing them to remain hidden from their prey. They fed ultra-


Figure 1. Confirmed unprovoked attacks by Carcharodon carcharias in the eastern North Pacific, 1926-2003, adapted from McCosker and Lea (1996). Those attacks in which Carcharodon is implicated but not demonstrated are identified by "?". Attacks during or after October, 1993, are identified by " ".
sonic transmitters to four individuals (3.7-4.9 m approximate total length) that were clearly large enough to have shifted from benthic prey to surface pinniped prey (Tricas and McCosker 1984), and of the size typical of encounters with humans. They also discovered that an inverse relationship exists between shark length and activity pattern, such that large sharks patrol within limited, particular areas, whereas smaller individuals did not restrict their movements. Martin et al. (2005) published a long-term study of 2088 observations of predatory events by white sharks in South Africa upon Cape fur seals (Arctocephalus pusillus pusillus) as well as shark attacks upon seal-shaped decoys. Kelly and Klimley (2003) briefly described a pilot study in which they observed C. carcharias at Point Reyes in north central California. Anderson and Goldman (1996), using photographs of white shark dorsal fins, were able to demonstrate the movement of two white sharks along the California coast. One was photographed at SFI in 1988 and not seen again until 1994, when it was photographed off Newport Beach, CA, $>700 \mathrm{~km}$ to the south and 250 km south of Point Conception. The other shark was photographed at SFI in 1991 and resighted in 1994 at Tomales Point, $>70 \mathrm{~km}$ to the north. Their work indicated that some sharks travel and that dorsal-fin appearance, like the caudal fin of some whales, is a useful character for identifying individuals. Martin (2005) described the distribution of white sharks in the northeastern Pacific, extended their known range to the central Bering Sea, and suggested that C. carcharias is more abundant off British Columbia and Alaska than previously suspected. He was unable to correlate their northerly distribution with El Niño or La Niña events between 1961-2004. A remarkable discovery of white shark movements was made in 1999 (Boustany et al. 2002) when four of six adult white sharks that had been tagged off the central California coast moved well offshore in a southwesterly direction; one of them travelled as far as Hawaii. Boustany et al.'s (2002) preliminary results suggested that at least some $C$. carcharias have a much wider range than had been assumed, and that they occupy an inshore continental shelf regime as well as an extensive pelagic phase. Pardini et al. (2001), using mitochondrial DNA of southern ocean white sharks, demonstrated that dispersal is sex-biased, with females probably being philopatric (non-roving) and males roving great, even transoceanic, distances. Their data and conclusions, however, contrast with those of Anderson and Pyle (2003), who found that in a 14-year study of 22 distinctively marked white sharks ( 239 observations made), individual males often occurred every year at SFI, whereas females were observed every other year at most. They concluded that in California, white sharks travel significant distances during a biennial reproductive and birthing cycle, whereas males travel shorter distances, if necessary, in order to copulate. Subsequently, Bonfil et al. (2005) demonstrated that Southern Ocean white sharks do make transoceanic migrations. Sharks that they tagged migrated between South Africa and Australia with remarkable speed and navigational abilities, dove to depths as great as 980 m , tolerated water as cold as $3.4^{\circ} \mathrm{C}$, and confirmed that C. carcharias is philopatric. And finally, Estes et al. (2003) updated previous studies of white shark predation on southern sea otters (Enhydra lutra nereis) in California. They reported that the number of shark-bitten sea otter carcasses (expressed as a percentage of the otter population) has increased significantly between 1968-1999. They did not, however, attempt to relate this increase to any change in the California white shark population or any oceanographic parameter. The above-summarized references provide indirect but useful information in attempting to understand the normal behavior of Carcharodon carcharias and thereby interpret their interactions with humans.

## Methods

In this study, we have relied upon unpublished reports, newspaper articles, and interviews with victims, witnesses, and other experts; in most instances we sent a standardized, 4-page form devel-
oped by us, and in many, but not all, instances it was returned. We have been selective in our decision as to which unprovoked attacks to include: we do not doubt a number of anecdotal instances described to us during the last decade whereby the boards of surfers have been bumped or brushed by sharks, most probably Carcharodon carcharias. In such cases, however, we lack adequate evidence to demonstrate clearly that an "attack" did or might have occurred, and unless the shark attacked and bit the board and/or its rider causing mechanical and/or bodily harm, we have not included it in our analysis. In several instances, we have more extensively described those incidents that are particularly instructive or that have been misrepresented in media reports. Enumeration of incidents prior to 1984 follows that of Lea and Miller (1985) and that of our previous report (McCosker and Lea 1996). We continue with our numbering system such that the attack on R. Williams in California is assigned "California 70" and the attack on R. Mackenzie in Oregon is assigned "Oregon 11." We herein define the short surfboards (generally shorter than 120 cm ), variously known as "boogie-boards", "belly-boards", "spongers", or "body-boards" as "bodyboard." Although we give measurements in metric units, nearly all victims described their experience in terms of English foot/pounds. We have either not converted those measurements when quoting victims and witnesses or have done so and rounded them so as to avoid creating an incorrect impression of precision. And, we advise caution with regard to the accuracy of estimates of distance from shore and depth of water made by the victims and/or other respondents.

## Verified Unprovoked Attacks

## In California

70. Robert Willianis, surfer; 30 October 1993; Humboldt County, Bunkers, Eureka. This account is based largely on Collier (2003) and an article from the Eureka Times Standard (1 November 1993).

Williams, a 26-year-old male Caucasian. was wearing a full black wetsuit with gray markings on its arms and legs, and used a 2 m triple skeg white surfboard with a yellow and green design on the top rails. He entered the water at about 1530 and was attacked at about 1630 . He was 200 m from shore, water depth ca. 7 m , at a surfing beach called "Bunkers," located 0.8 km north of the Eureka breakwater jetty. The swell was ca. 1 m , the sea surface calm, water temperature ca. $10^{\circ} \mathrm{C}$, air temperature ca. $16^{\circ} \mathrm{C}$, and the water visibility $5-6 \mathrm{~m}$. The victim recounted seeing several pinnipeds in the surf very close to shore as he entered the water (Collier 2003).

Collier (2003:144) quoted Williams" account of the event: "Five other surfers had gone out about 15 minutes before I got into the water and were waiting for a decent wave. They were talking when I pulled up to them. I paddled away from this group about 15 yards and waited several minutes before I saw a nice set [of waves] building. I began paddling out to catch the set when, all of a sudden, there was a surge of water that pushed me up into the air. I saw the shark at this moment for a fraction of a second. The shark grabbed my legs and board, pulling me underwater 3 to 4 feet. I hit the nose of the shark, which did nothing. Then I saw its eye, so I jammed my thumb in as far as I could." The shark then released the surfer. swam seaward at a downward angle, shaking its head from side-to-side. The victim had resurfaced a few meters away from his board, climbed onto it, and realized the severity of the wounds to his left leg. He called to nearby surfers who then assisted him to shore. He was driven to St. Joseph Hospital in Eureka where he arrived in shock but alert. He was treated for a severe wound to the middle of his left thigh and lower leg which involved muscular, nerve, and vascular damage.

The attacking shark was estimated to have been 4-5 m in length and, based on the attack sce-
nario, location, and the injuries, was most probably Carcharodon carcharias. A subsequent attack occurred at precisely this location on a surfer on 4 November 2000 (see \#82, C. Stewman).
71. Janes Robinson, diver at or below the sea surface; 9 December 1994; San Miguel Island. Fatality. This account is based on wire service reports, RNL's discussions with the Santa Barbara County Coroner's Office, advice from Burr Henneman (in litt. 15 Mar. 2001) and Tom Kendrick, a commercial urchin diver and associate of the victim (pers. commun. April 2005), and Collier (2003).

Robinson, a 42-year-old male Caucasian, was a commercial sea urchin diver. He was aboard the F/V Florentia Maria, a $34^{\prime}$ fishing vessel outfitted to support hookah diving. She arrived and anchored ca. 300-400 m off Castle Rock near Westcott Shoal, ca. 2.2 km off the northwest end of San Miguel Island, at about 0900 . The sky was overcast and the sea was calm. Robinson entered the water (ca. 5-6 fms depth) using an electric scooter to check the boat's position on the reef, then returned to the surface to inform the crew to drop the anchor. He was clothed in a full black neoprene wet suit with gloves and booties. He then returned with the scooter to the bottom to collect urchins while his tenders were forward on the boat. They heard the diver call out "Hey, hey" from the stern and discovered that Robinson was attempting to pull himself onto the dive step and had been bitten by a shark. They pulled him onto the deck and observed a $3-4 \mathrm{~m}$ diameter blood stain in the water. Collier (2003: 148) reported that "the diver had been in the water about 15 minutes, but had been submerged only three to four minutes during his second dive before calling out." It was not clear whether his attack occurred at or beneath the surface. A tourniquet was applied and towels were placed over the wound. He began to lapse into unconsciousness after about 15 minutes and he was given CPR by the crew members. A 911 call was made and a US Coast Guard helicopter arrived ca. 30 minutes later and flew him to Goleta Valley Hospital in Goleta. Upon arrival he was given electroshock treatment by the emergency room physician, but he did not revive. Collier (2003: 148) described the wounds as follows: "he had received a single bite to the upper right leg, involving the hip and thigh. The crescent-shaped wound extended onto the anterior surface of the left thigh, terminating at the level of the right knee joint. This arc measured 45 cm at its widest dimension, from the thigh to the knee. Wound dimensions and interspace measurements were comparable with the dentition of a White Shark 5 to 5.5 m in length. Unfortunately, the wounds suffered during the attack - including massive loss of tissue, severing of vascular vessels, and the almost complete amputation of the right leg at the knee - were too severe to be treated effectively. . . ." A tooth, later confirmed to be that of a Carcharodon carcharias, was removed from the victim's femur.

This represents the third known attack upon a human by a white shark in the general vicinity of Castle Rock and Westcott Shoal, and the fourth occurred to the east at Harris Point, San Miguel Island. San Miguel harbors several large colonies of pinnipeds.
72. Unidentified adult female, kayaker; 24 June 1995; San Diego County, La Jolla Cove. Sketchy reports of a young woman attacked while kayaking at La Jolla Cove indicate to us that an unprovoked white shark attack did occur, however we are unable to verify most of the purported details and thereby remain somewhat dubious about this incident. We base our report on discussions with R. H. Rosenblatt of the Scripps Institution of Oceanography and the newspaper articles published in the San Diego Union Tribune (7 July 1995 by Cheryl Clark and 8 July 1995 by Terry Rodgers and Mark Sauer).

The victim, a 19-year-old woman, was reported to have been kayaking along the kelpbeds off La Jolla Shores in the vicinity of La Jolla Cove. Four of her friends were boating in a dinghy nearby at the time. Clark reported after interviewing the treating physician, Joel Berger, that "Between 7:30 and 8:30 p.m., something went under the kayak and struck it, causing the woman to fall into
the water. She was bitten in the head before her companions pulled her into the dinghy, Berger said. The woman suffered lacerations to the head and face and was treated at an urgent care facility." The doctor declined to release the woman's name. Rodgers and Sauer reported that Berger, a face specialist, "found an unusual wound pattern - three separate cuts on one side of the head and a deeper cut on the upper cheek that penetrated a sinus. That indicates that the shark had most of the woman's head inside its mouth, said Rosenblatt, who interviewed Berger. . .about the attack. . . . The surgeon. . said . . .that he removed a one-inch tooth fragment from the woman's sinus." Although Rosenblatt did not see the fragment, on the basis of a drawing made by Berger, he proposed that the tooth was that of a "white shark that was at least 10 feet long." Because the victim did not report the attack until two weeks had passed, and because he kept the tooth, we were unable to pursue this incident.

Unprovoked white shark attacks on humans are very rare south of Point Conception, California. The identity of the shark that attacked and killed Robert Pamperin (\#8) in La Jolla Cove on 15 June 1959 remains disputed (McCosker and Lea 1996:427). Although it is presumed to have been either a white shark or a tiger shark (Galeocerdo cuvier), McCosker and Lea (p. 427) concluded that "Lacking additional evidence, we suspect that the identity of the attacker may never be determined." In recent years, there have been occasional sightings of white sharks in the vicinity of Windansea Beach (ca. 1 km south of La Jolla Cove) and a white shark was observed consuming an adult pinniped about 1-2 km off the Children's Pool at La Jolla Cove on 19 Nov. 2002 (reported by E. Zieralski in The San Diego Union-Tribune, 30 Nov. 2002). The dramatic increase in the pinniped population at La Jolla Cove during the last decade may well explain the current presence of white sharks at that location; however, white shark sightings hadn't been reported during the 1959 and 1995 incidents.
73. Marco Flagg, scuba diver; 30 June 1995; Monterey County, Point Lobos State Reserve, Whaler's Cove. This account is based primarily on the extensive and widely circulated report filed by Flagg over the internet on 2 July 1995, as well as a media report (Davis 1995) and JMc's and RNL's conversation with the victim and correspondence with T.C. Tricas (then of the Florida Institute of Technology), C. Lowe (then of the University of Hawaii), and H. Mollett and D. Powell (Monterey Bay Aquarium).

Marco Flagg, a 31-year-old male Caucasian and experienced scuba diver, was attacked in midwater off Whaler's Cove, a popular Central California diving site. He and two friends, Steve LeCompte and an unidentified woman, made two dives that day, the first commencing at 1445. They dove from a 12.5 ft Zodiac inflatable boat, anchored about $350-400 \mathrm{yds}$ from shore in 90 ft . The bottom was characterized by rocky outcroppings interspersed by sand channels. There was kelp in the vicinity but not at the attack site. Pinnipeds were observed basking on large rocks within the cove. The sea was calm, with no swell and minimal wind. Surface light was reduced due to low clouds and the late afternoon time of the dives. Visibility was 10 ft at the surface and improved to 30 ft at the bottom. Flagg was wearing a $1 / 4^{\prime \prime}$ blue-striped black neoprene wetsuit, a black hood, booties and fins, and a yellow/orange 22 lb weight belt. Attached to his high pressure hose was a "DiveTracker DTX" instrument console housed in an $8^{\prime \prime} \times 3.5^{\prime \prime} \times 2.5^{\prime \prime}$ aluminum box with $1 / 4$ " aluminum wall strength. which rode at the level of his abdomen. His first dive, between 1445 and 1535, was to 98 ft and without incident. He buoyed the dive site, returned to shore for lunch, and returned to the buoy at 1720 to make a second dive. During this dive Flagg employed a white scooter (an electric diver propulsion vehicle). Propelled by the scooter, he descended at ca. $20^{\circ}$. After ca. two minutes and at a depth of ca. 50 ft . Flagg reported that he looked to his right "and saw the massive pectoral fin attached to the end of a torpedo shaped body of a large fish. The fish was at a distance of maybe 20 ft , at the edge of visibility. The sighting lasted for two to three seconds before
the animal disappeared from view in the cloudy water." Flagg turned the scooter and propelled himself toward the boat. At 40 ft depth, $15-20$ seconds after the shark sighting, Flagg reported that he looked to his "left and below and saw the massive, wide open, near circular, teeth-lined mouth of an animal coming at me. The mouth appeared to have a diameter of certainly more than two feet but most likely not more than three feet. . .and shortly (ca. one second) thereafter felt a severe but dull pressure on my body. I do not recall being shaken by the animal nor taking any significant evasive or defensive action. Instead, I appeared to be free from its hold after maybe two seconds." He then used the scooter to return to the Zodiac at maximum speed, surfaced about 20 yds from it, and continued at the surface. Upon reaching the boat he dropped the scooter, attempted unsuccessfully two or three times to climb into the Zodiac while wearing his tank and weight belt. He then released the belt, removed his tank and buoyancy compensator, and climbed aboard, but fell in while attempting to retrieve his gear. He climbed back in and revved the outboard in short bursts to inform his partners. Although he had suffered cuts to his left arm, abdomen, and leg, he remained conscious and was aware that he had not suffered massive blood loss. His partners soon surfaced and they returned to shore where an ambulance transported him to the Community Hospital of the Monterey Peninsula. There he was treated by Dr. Blynn Shideler for a 1.75 inch diameter cut to his left forearm (requiring six stitches), a cut on his upper left leg (eight stitches), and a wound to his lower left abdomen (two stitches). Flagg noted that "the distance from the leg wound to the arm wound is 20 inch if my arm is down and 30 inch if my arm is extended at a 45 degree angle up (while standing). I do not specifically recall what position my arm was in when the animal bit. The fact that I was using the scooter at the time suggests that it should have been 'up'." He was given antibiotics at the hospital and, other than experiencing a slight fever, quickly recovered. Flagg hypothesized that he experienced only minor injuries either because "the shark . . . simply decided to not exert much force on my body . . . or that (he was) sandwiched between two layers of metal . . . the tank on (his) back and the Divetracker instrument on (his) front . . . (such that) the pressure on the tank and on the Divetracker spread the force of the bite over a large area. . .resulting in the bruise on my abdomen."

Flagg's incident is extraordinary for several reasons: a) he was attacked while scuba diving in midwater (an uncommon white shark attack scenario); b) he saw the shark prior to the attack. His female diving companion also saw the shark while she was underwater - "it was like a freight train going by underneath me" she said (Davis 1995); and c) he was using an electric diver propulsion vehicle. It is well known that sound (Myrberg 1978) and electric fields (Tricas and McCosker 1984) can be attractive to sharks and some have suggested that the scooter may have been responsible for the shark's behavior. Discussions with shark behaviorists/physiologists T.C. Tricas and C.G. Lowe suggest that the sounds emitted by the electric propulsion device could have attracted the shark. Lowe reported that carcharhinid reef sharks in Hawaii that were attracted by operating propulsion scooters would move away when the devices were turned off. Tricas calculated that although the sound may have attracted a white shark, it was unlikely that the electric field created by such a device would be strong enough to project more than a few cm beyond the object's surface.
74. Bryan Hillenburg, breathhold abalone diver; 3 Sept. 1995; Humboldt County, Shelter Cove. This account is based on conversations with Tobias Young, a reporter for the Santa Rosa Press Democrat who had considerable contact with the victim, and RNL's examination of the shark tooth fragments. We were unable to communicate with the victim.

The victim, an adult male 30 -year-old Caucasian, was free diving for abalone at Shelter Cove in ca. 30 ft of water. He and his partner, an adult male, were wearing wet suits and had been diving for about three hours and had swum into a "seal rookery." The victim had made a dive to the bottom and captured an abalone; at 1630 he surfaced and was leaning on his kayak and placing the
abalone in a dive bag when a shark bit into the bottom of his left leg and swam to the surface. The victim pulled his leg and foot from the water and observed the shark. Tobias reported that "the shark then swam down and tugged at Hillenburg's leg before letting go. (His) diving partner . . . Michael Burns . . . was surfacing when he saw part of the shark's body - from behind the gills to the tail fin - swim away after the attack." His partner aided him at that time and tried to control the bleeding. Three nearby (ca. 50 yds ) breathhold abalone divers had finished diving and were in a small aluminum skiff. Tobias reported that they "saw Hillenburg swim frantically back to his kayak and climb out of the water." Hillenburg and his partner entered the skiff and towed the kayak to shore. They were able to control Hillenburg's bleeding and he was then taken by ambulance to a hospital. The bite was deep into the victim's calf (a tooth penetrated the bone) about 10 cm above the ankle. Four teeth remained imbedded in his leg and were removed during surgery. The largest tooth was 14 mm long and 9 mm in width with fine marginal serrations, clearly that of a white shark. Fifty staples were applied to the victim during the $3 \frac{1}{2}$ hour surgery, which involved the repair of torn flesh, tendons, and nerves. Tobias reported that "a great white estimated at 12 -feet long had been seen several times in the area," and Jerry Hartman, the Shelter Cove Fire Chief, related that "we do have a great white that stays here." One previous white shark attack (CA \#64, D. Abernathy) occurred at Shelter Cove on 4 Dec. 1991, involving a hookah diver at the surface.
75. Michael J. Sullivan, windsurfer; 29 September 1995; Santa Cruz County, Davenport Landing, ca. 24 km north of Santa Cruz. This account is based on advice from S. Van Sommeran, G. Balazs, foreign newsclips, and Collier's (2003) report.

Sullivan, a 25 -year-old male Caucasian, was riding a 2.5 m lime-green sailboard with a clear Mylar sail trimmed with a red and black margin. He wore a black wetsuit. The sky was clear and sea conditions were rough with $2-3 \mathrm{~m}$ waves caused by a 20 kt northwesterly. Sullivan said that he usually saw pinnipeds at that location but saw none on that day. Collier (2003:153) reported that "several dense kelp canopies were 100 m south and shoreward of the attack location, but there were no kelps in the immediate area . . . " Sullivan entered near the lower reef at Davenport Landing at 1645 and had been windsurfing with approximately twelve others. Due to reduced wind conditions, Sullivan turned toward the shore, his speed about $5-8 \mathrm{kts}$. At that point the board and rider were lifted by a shark and Sullivan fell upon the shark's back. The shark then shook the board free from its teeth and slapped its tail wildly; Sullivan then swam about 10 m before turning to investigate his board. The shark had left and Sullivan then swam back to his board, righted it, and sailed to shore. His only injury was an abrasion on the top of his right foot. Sullivan and other observers estimated the shark's length to be ca. 4 m . Considering the shark's behavior and its size and its locality, it is unlikely that it was other than a white shark.

This represents the first verified attack on a windsurfer by a white shark. An attack upon a windsurfer (Tony Donoghue, 30 May 1999) off South Australia's Yorke Peninsula may well have involved a white shark; however, only the shredded wetsuit, scratched sailboard, and torn harness of the missing victim were recovered, so it is impossible to know the behavior of the shark or the victim at the time of attack. Other attacks on windsurfers, such as that on Jean Goenvec on 15 August 2000 at Kanaha Beach, Maui, would be better categorized as "an attack on a paddleboarder." Mr. Goenvec, presumably attacked by a tiger shark (Galeocerdo cuvier), was not underway but rather was sitting on his board with his legs dangling when one leg was severely bitten.
76. Colum Tinley, breathhold surface abalone diver; 13 August 1996; Marin County, Tomales Point, Bird Rock. This report is based on the victim's report to us, including photographs of the removed tooth fragments. several newspaper articles. and a report filed by Ralph Collier on the Shark Research Committee website (<www.sharkresearchcommittee.com>).

Tinley, a 35-year-old male Caucasian, was attacked while freediving for abalone on the south
side of Bird Rock, located southwest of Tomales Bluff. (His age has been variously reported as 35 , 36. or 37 . His 36 th birthday occurred the day after the attack. Other reports erroneously cited the location as within Tomales Bay; it was outside and south of the bay's entrance.) Tinley was diving along with two other adults (Karol Knox and Charles Wilson) using a 4 m inflatable Avon boat. They had made several dives along the east side of Bird Rock and then relocated to the south side. Collier reported that "Tinley was 30 meters from shore in water 5 to 6 fathoms deep with 5 meters of visibility and a estimated temperature of $12^{\circ} \mathrm{C}$. The ocean floor was primarily rocky, with some scattered short-stature kelps. The sea was calm with a 0.5 -to- 1 meter groundswell. The sky was overcast and foggy with a temperature of about $16^{\circ} \mathrm{C}$. ." At 1110 , Tinley, alone, spent 5 minutes diving from the Avon and collected two red abalone. He surfaced, examined a third abalone, then dove to about 6 m depth and observed a large white shark, $4-5 \mathrm{~m}$ in length by his estimate, beneath him. The shark turned, rapidly ascended and bit the victim who had by then attempted to push away from the shark by extending his arms. The shark lifted him, then released him, bit him again, then released him and swam away. From the boat, Wilson observed the shark coming out of the water with Tinley, its tail thrashing, and then releasing the victim. Wilson estimated the attack to have lasted 7 seconds. Bleeding profusely, Tinley swam 5 m to the boat and was assisted aboard. Once aboard, the Coast Guard was called by VHF radio and a Sheriff's Department helicopter was dispatched quickly. Tinley was airlifted to Santa Rosa Memorial Hospital where he arrived and was treated approximately 75 minutes after the attack. Collier described the injuries: "He had received five tooth lacerations involving the deep tissue of his left shoulder, six lacerations to his left forearm, two lacerations of his left hand, and a large cut to the left side of his lower abdomen. Several hours of surgery was required to repair the damage to Tinley's nerves, ligaments, tendons, vascular vessels, and the soft tissue of his shoulder, arm, hand, and abdomen. During the operation, surgeon James Harwood removed three small tooth fragments from the laceration in the diver's left shoulder. The fragments not only substantiate Tinley's identification of his attacker, but also assist in determining the length of the attack shark to be about 6 meters."
77. Mark Quirt, 5 Oct. 1996, surfer; Marin County, Dillon Beach, Lawson's Resort. This account is based on a communication through the internet with Mr. Stuart Dole, a close friend of the victim, and on an article published by Anne Baker in the Point Reyes Light on 10 October 1996. The victim, a 22-year-old male Caucasian, was surfing at 0930 with his father and six friends near rocks north of Lawson's Resort day beach, in the vicinity of Dillon Beach. Wave height was "overhead" and water depth was 10 ft . The victim was straddling his board when attacked. His father, Steve, was 50 ft away and heard the victim scream "shark." The father described the shark as very big, with a dorsal fin more than three ft tall. Another nearby surfer said he saw the victim's leg in the mouth of the shark. The father helped Mark back onto his board and got him aimed towards shore, and stayed with him all the way in. Dole reported that "the shark circled very close to them after the attack - Mark looked right into its eye - he 'saw its face.' When it swam off its wake was like a submarine." A surfer in the group was a physician and started an intravenous fluid injection about 15 minutes after the attack. A Fire Department rescue team arrived very quickly and a helicopter then transferred him to Santa Rosa Memorial Hospital. Emergency Medical Technician Steve Truttman attended to Quirt and reported that the victim was bitten on the left leg, suffering incisions up to 3 " long from his ankle to his knee, as well as a puncture wound to his right hand from trying to fend off the attack. Truttman said that it was "as if someone had taken a straight-razor and made slash marks diagonally across the flesh almost to the bone." Stuart Dole, an associate of Quirt's, reported that "no major tendons, nerves, or blood vessels were cut, despite massive muscle shredding. His brand new wetsuit was shredded . . . it cut the leash too." It is remarkable that despite the traumatic wounds that Quirt suffered, none of his major tendons, nerves, or blood vessels were
cut. He was hospitalized and received 180 stitches. Quirt's attack occurred two days after a shark is said to have bumped a surfer at Salmon Creek, approximately 14 km north of Dillon Beach. Neither the surfer nor the board were damaged in that incident and we have not included it in our listing of unprovoked attacks.
78. Greg Ferry, surfer; 29 November 1996; Sonoma County, Salmon Creek. This report is based on JMc's telephone conversations (2-3 December 1996) with the victim and Rob Robinson, a surfer with Ferry at the time of the attack, the victim's response to our forms, and an article by Eileen Clegg, Santa Rosa Press Democrat (30 Nov. 1996).

Ferry, a 45-year-old Caucasian, and Robinson and Robinson's brother entered the ocean at 0730. Ferry was bitten at 0830 . He was wearing a thick black O'Neill neoprene wet suit and black booties; his hands were exposed. His surfboard was an 8 ft Maury Doyle cloud cell board (not fiberglass) with a single skeg and a square tail. It was blue above and yellow below. The other surfers were riding 8.5 ft and 9 ft teardrop-shaped boards. The water was cold, its visibility ca. 1 m , the sky was clear, there was little or no wind, and the surf was ca. 1.3 m in height. Salmon Creek was dry at its ocean entrance. No marine birds, pinnipeds, or other wildlife were seen in the area. No other surfers were in the water. Ferry and the Robinsons went ca. 200-300 m offshore to the breaking surfline. The other two were 10 m shoreward of Ferry, one ca. 25 m south and the other ca. 45 m to the north. Ferry pushed through a wave, kicked to get back up on his board, and felt a sharp pain to his left ankle. He suspected that his left leg had brushed against a shark's open mouth as it attacked the board. A single tooth cut his left ankle very cleanly but not deeply. The shark continued to bite the board, thrashed twice, became momentarily entangled in Ferry's leg leash, and then departed. Ferry did not see the shark at any time and the others saw none of the event. Ferry then rode a wave to shore and was taken to Palm Drive Hospital in Sebastopol where Dr. Peacock applied 8 stitches to a clean laceration on his left ankle. Peter Klimley examined the tooth impressions left in Ferry's surfboard and estimated the attacking shark to have been a $3-5 \mathrm{~m}$ white shark.

Salmon Creek is a popular surfing location and the site of previous (\#13, D. Vogensen, swimmer 20 Aug. 1961) and subsequent ( $\# 85$, M. Casey, bodyboarder 28 Nov. 2002) white shark attacks.
79. Scott Yerby, surfer; 24 August 1997; Humboldt County, Moonstone Beach, directly off the mouth of the Little River. This incident was incorrectly reported by some news media as having occurred at Clam Beach, which is the long expansive beach south of Moonstone. This account is based on the form returned to us by the victim, an article written by Rhonda Parka, Eureka Times Standard (25 Aug. 1997), and Collier (2003).

Yerby, a 29-year-old male Caucasian, was wearing a full black neoprene wetsuit and used a surfboard with a white underside and blue top. Yerby reported that the sky was clear, the air warm, the sea calm, the tide had ebbed $(-1 \mathrm{~m})$ and the water was warmer and clearer than he was accustomed to at that location. Yerby and a companion, David Yun, paddled out over a channel to ca. 70 m from shore; they were ca. 50 m apart. Between 1300-1330 Yerby left his board to discover the water depth ( ca .2 m ), then returned to his board and sat upright upon it just beyond the surfline. Collier (2003: 159) reported that "there was a splashing sound as the shark struck his surfboard, left leg and hand, biting deeply into the leg. The shark came up out of the water, shaking the surfer violently for several seconds. Yerby struck the shark's head with his right hand, whereupon it released its grip and swam off. The shark was not seen again." Yerby, assisted by Yun, paddled to shore. Upon arrival they were aided by two emergency medical technicians and a nurse who were picnicking on the beach. They administered first aid and then carried him to a nearby ambulance which transported Yerby to Mad River Community Hospital in Arcata. Yerby was alert and not in shock upon arrival, whereupon he was treated for severe lacerations to the tendons and muscles of his left hand and leg. He had lost ca. 5 pints of blood by the time he arrived at the hospital. Teeth had pen-
etrated his leg to the femur and tibia and the wounds were arranged in a large crescent.
Three shark tooth fragments were removed from his tibia and they, along with the measured intertooth distances, indicated that the attacker was an ca. 4-5 m white shark (Yerby estimated the shark to be $3-4 \mathrm{~m}$ in length). The location of the attack, Moonstone Beach at the mouth of the Little River near Eureka, has now experienced four white shark attacks upon surfers.
80. Jonathan Kathrein, bodyboarder; 26 August 1998; Marin County, Stinson Beach. This report is based on numerous conversations by JMc with the victim and the victim's family members, a telephone interview with lifeguards and a physician at the site and time of the attack, and is also taken from newspaper accounts.

Kathrein, a 16 -year-old male Caucasian, $5^{\prime} 11^{\prime \prime}$ tall and 155 lbs , was bitten while riding a bodyboard along the southern shore of Stinson Beach. This general location is perhaps the most-frequented beach by bathers, surfers, and bodyboarders in the San Francisco Bay Area, and although white sharks have been observed from the water by boaters, fishermen, and from the shoreline, this is the first known unprovoked attack at that site. The victim, an athletic, robust and healthy high school student, was ca. 50 m directly offshore from the south lifeguard tower. He rode a Morie bodyboard, 107 cm in length, 50 cm wide, and 6.4 cm thick. It was bright yellow above and orange below, with a turquoise band on its lateral margin. A black 1 m elastic cord was attached from the board to his wrist. He wore a blue and black neoprene wet suit (blue covering his upper body and buttocks, black from thighs to knees) that ended before his knees and wrists. He was not wearing fins or a watch. The sky was partly cloudy and overcast, but fog-free. The water was fairly dirty with visibility estimated at ca. 1 ft . Wave height was ca. $3-4 \mathrm{ft}$. There was no notable weather change while he was in the water. He entered the water at 1345 , paddled south and parallel to shore, caught a wave, swam offshore again, and rested upon his board for five minutes, and then contacted a firm object alongside his board about 1 ft beneath the water with his right hand. He looked, saw nothing, began to paddle, and 6-8 seconds later a shark rose from beneath his right side, flipped him and the board over, and held him underwater for ca. five seconds while "thrashing its head" several times. The victim recalls grabbing the shark's gills and inserting two fingers into its gill slits, at which point the shark released him. Still attached by leash to his board, he mounted the board, swam ca. 125 ft to knee-deep water without stopping, at which time rescuers took him ashore and applied first aid. He was then helicoptered to a trauma center. His injuries were traumatic and required more than 300 stitches. A single wound of 47 cm width on the back side of his right thigh cut through muscle and tendons and penetrated to his femur. The tooth insertion scars are ragged; the upper jaw apparently penetrated his flesh from his dorsal hip surface to the top of his knee, the lower jaw teeth penetrating the anterior portion of his knee. There was no significant tissue loss and no damage to his nervous tissue. Neither teeth nor tooth fragments were left in the victim or his board. Based on the attack scenario and the appearance of his wounds, we have no doubt that Mr. Kathrein was bitten by a white shark. The width of the bite scars on his right thigh would indicate that the shark was about $3.5-4.5 \mathrm{~m}$ in length.

McCosker visited the attack site the following week and discovered an adult male California sea lion (Zalophus californianus), dead along the shoreline, that had been bitten in midbody by a white shark. Sightings of white sharks from the shoreline by lifeguards and beach visitors kept the beach closed for several days following the attack on Kathrein. The following year, at approximately the same period, video photographs taken by a beach visitor near the lifeguard tower at Stinson Beach clearly evidenced an adult white shark swimming at the surface beyond the breaker zone. The beach was again closed. At the time of this writing Mr. Kathrein is again healthy, robust, and swimming regularly.
81. Paul "Peck" Euwer, surfer; 29 September 2000; San Mateo County, Pillar Point,

Mavericks. The investigation of this attack is based on the form returned to us by Euwer, interviews by JMc with Michael Kasic, a fishery biologist who was surfing alongside the victim during the attack, an analysis of Kasic's photograph's of the victim and his surfboard after the attack, and additional information that was posted on the internet under: sharksurvivor.com/interviews ("'Peck' Euwer, California, USA"); surfline.com ("Sneaker set"); and mavsurfer.com ("Mavericks defines the food chain" by Jake Howard).

Euwer, a 34 -year-old male Caucasian, $6^{\prime} 0^{\prime \prime}$ tall, 180 lbs , was attacked at 0900 while paddling his surfboard to the surfbreak at Mavericks, a location know for its very large surf and an offshore break. The day was described as "opening day" in that the wave heights had increased (to about 4 m ) on that day. The water visibility was poor (ca. 60 cm ) and the water temperature about $13^{\circ} \mathrm{C}$. Euwer was joined by two adult male surfers, Michael Kasic and Mark Sponsler, who were preceded at some distance by four other surfers. Sponsler, an experienced Mavericks surfer, was riding a $274-\mathrm{cm}$ board and went ahead of Euwer and Kasic. Euwer was on a $211-\mathrm{cm}$ fiberglass surfboard that was white with three blue skegs. Kasic was on a longer ( 241 cm ), more slender board that had three black skegs. Euwer's and Kasic's boards were attached to the surfers' ankles by leashes. Both were wearing black full wet suits but wore neither gloves nor booties. Euwer was wearing a wedding ring on his left hand and a black Timex digital watch that was mostly covered by his wetsuit sleeve. Kasic related that they passed " 6 or 7 harbor seals" (Phoca vitulina) and they paddled beyond the nearshore rocks; Kasic was ahead of Euwer as they passed "Mushroom Rock" by ca. 100 m (ca. 1 km from shore), and they paused for about a minute with their legs dangling. They then began paddling, with Kasic about 6 m to Euwer's side and slightly ahead of him when Kasic heard a loud thump ("like a watermelon hitting cement") and turned to see the lower jaw of a large shark bite the underside of Euwer's board and lift the board and rider about 1 m in the air. As Euwer held the nose of the board, his legs were hinged above the board, and the shark then bit the topside of the board with its upper jaw teeth. Euwer then fell on the shark's nose and slid along its back beyond its first dorsal fin and then, at the level of the caudal peduncle, he slipped off. The shark, with its mouth open, then swam toward Kasic and descended beneath him; its dorsal fin at that time was 2 m from Kasic. Both Euwer and Kasic clearly presumed that the shark had risen nearly vertically (rather than from the side) when it first struck the board. Euwer was unhurt by the attack but the left leg of his wetsuit had been punctured by the shark's lower jaw teeth as it raked his leg. The board (Fig. 2) evidenced deep raking grooves on its underside and the topside had a 36 cm wide arc from the upper jaw teeth. Euwer and Kasic remounted their boards and paddled rapidly ca. 400 m to shore, and did not see the shark again.

The vicinity of Mavericks includes a rocky coastline and modestly protected embayments, and is inhabited by numerous resident pinnipeds (mainly California sea lions and harbor seals). Jake Howard of mavsurfer.com quoted


Figure 2. P. Euwer displaying the underside of his 211 cm surfboard that was bitten by a white shark. (Photograph by Debra Goodshall. Half Moon Bay Review.)

Frank Quirate's (a Rescue Boat Operator at Mavericks) account that "the rocks where he was hit is home to a pod of seals, including some huge bulls that patrol that very area . . . There was video shot of two whites chomping on a whale carcass that was filmed a year ago just north of Mavericks. A kayaker last year reported a great white cruising past his twelve foot kayak and dwarfing it." Howard added that "last winter also presented Pacifica locals with a treat as a great white hit a seal in the middle of the line-up. Most recently a kayaker spotted a shark around Mushroom Rock just a week prior to the attack." In consideration of the location, the conditions of the attack, and the dental pattern left in Euwer's surfboard, it is obvious that the attacking shark was Carcharodon carcharias.
82. Casey Stewman, surfer; 4 November 2000; Humboldt County, Bunkers. This report is based on newspaper reports. We were unable to contact the victim.

Stewman, a 27-year-old male Caucasian, was surfing north of the North Jetty of Humboldt Bay. His board was white and 224 cm long. He spent about an hour surfing before he moved farther north, ca. 0.9 km , to an area known as the Bunkers, which was less crowded. He was about 250-300 yds offshore in water $10-15 \mathrm{ft}$ deep for about 30 minutes (ca. 1630) when he sensed something beneath him. The board was then hit directly from below by a shark that grasped his legs and the board, and pulled them into the water. The shark almost immediately released the victim and the board and apparently swam off. The victim, separated from his board, now floating upside down, grabbed it and pulled himself onto it, then paddled and rode a wave to shore as quickly as possible. He was treated as an emergency patient at Mad River Hospital for wounds to both thighs, which required 31 stitches. The shark, although not seen clearly, was estimated to be $8-10 \mathrm{ft}$ long. Based on the shark's behavior and the condition of the wounds we presume that the attacking shark was a white shark.

The attack on a surfer on 30 Oct. 1993 (\#70, R. Williams) also occurred at this locality, north of the North Jetty of Humboldt Bay.
83. Lee Fontan, surfer; 31 May 2002; Marin County, Stinson Beach. This report is based on conversations by JMc with the victim's father, the victim, and with a surfer who was alongside the victim, and is also taken from newspaper accounts.

Fontan, a 24 -year-old male Caucasian, $5^{\prime} 7^{\prime \prime}$ tall and ca. 175 lbs , was surfing ca. 50 m offshore from Seadrift at the south edge of the Stinson Beach/Bolinas Estuary Channel. It was a warm day with clear sky, the water was said to be warmer than usual, wind and swell from the south, surf height was $6-8 \mathrm{ft}$, and water depth was ca. 10 ft . Fontan rode a $6^{\prime} 8^{\prime \prime}$ yellow, triplefin fiberglass surfboard which had a "no sharks" decal on its underside. He wore a black neoprene wetsuit with hood and booties, but his hands were naked. He entered the water at noon, paddled beyond $12-15$ other surfers, and sat upright on his board with his feet (but not his hands) suspended and faced the sun. He was then lifted from the water by a $12-14$-ft shark (its size estimated by nearby surfer John Gilbert of Stinson Beach). Gilbert advised (pers. comm. to JMc) that "I looked over and this guy was about three or four feet out of the water in the shark's mouth. You could see its teeth, its gums. Its eyes were shut. Its gills were wide open, like shutters. The whole dorsal fin on its back was out of the water." The shark then released the surfer and swam away. Fontan did not see the shark prior to the attack and claims to have struck it on the snout during the attack. He was assisted to shore by nearby surfers and quickly taken by ambulance and helicopter to a nearby hospital. He required 100 stitches and suffered a 20 cm gash to his left thigh and wounds to his left shoulder and chest, and there were three obvious holes beneath his ribs. No teeth were left in the board or the victim. We assume from the attack scenario that it was a white shark. The victim has recovered and is surfing again.
84. Reed Richards, surfer; 22 September 2002; Humboldt County, Moonstone Beach. This
account is based on RNL's telephone conversation with Richards and a report from the Ukiah Daily Journal (21 Aug. 2004).

Richards, a 35 -year-old male Caucasian, was surfing off Moonstone Beach early Saturday morning. He was straddling his board just outside the breakers in about $8^{\prime}$ of water when he felt a tremendous force against his leg and observed a shark he estimated to be $10-12 \mathrm{ft}$ in length. The shark then bit into the front of the 6 ft surfboard and violently thrashed up and down several times. Richards described this as feeling "like a rodeo ride." At this time Richards' leg was pinned between the surfboard and the shark's side. Richards reached out and hit the shark in the head, at which time the board was released and the shark rolled away. Richards fell off the board and into the water. He was leashed to the board and immediately swam back to it, then caught a small wave that took him to shore. During this period he felt he was going to be hit again by the shark; however, the shark did not return. Other surfers in the area of the encounter also quickly exited the water. Several surfers and kayakers arrived later in the morning, entered the water at the site of the encounter, but did not observe a shark. Others, however, chose to stay out, at least for the day.

Richards was not injured but his surfboard was badly damaged. Moonstone Beach is the site of two previous attacks on surfers, on 18 October 1976 and 17 October 1980. This is the tenth sharkhuman interaction recorded in Humboldt County; six of these incidents involved surfers.
85. Michael J. Casey, bodyboarder; 28 November 2002; Sonoma County; Salmon Creek. This account is based on our conversations and correspondence with the victim and his wife, and his response to our report form within three weeks of the attack.

The location of the attack, Salmon Creek Beach, south of the town of Bodega Bay and just south of Bodega Dunes, is one of the most popular surfing locations in Sonoma County. Casey, a 48 -year-old male Caucasian, is $5^{\prime} 10^{\prime \prime}$ tall and weighs 175 lbs . He was attacked while bodyboarding ca. 150 yds from shore in water about 10 ft deep. He was wearing a black wet suit, booties and gloves. His board was 107 cm long, 56 cm wide, and 6.4 cm thick, and blue above and white below. The sky was clear, offshore winds were blowing, and the surf height was $3-4 \mathrm{~m}$. The water was relatively clear and about $12^{\circ} \mathrm{C}$. Neither kelp canopy nor pinnipeds were observed by Casey in the vicinity of the attack. (Other surfers did report seeing pinnipeds at this location on previous occasions.) The victim entered the water at about 0715 and had been surfing for $1.5-2$ hours. He advised us that "after catching a wave, I paddled back to the line-up. I was laying on my bodyboard, facing the horizon, waiting for the next set. My legs were dangling in the water. There were 4-5 other surfers within $15-20^{\prime}$ of me. I was not doing anything, i. e., paddling, swimming etc. All of a sudden, I felt this tremendous surge of power from beneath the water. And at the same time I felt a sharp pain in both my legs. I did not see the shark before the bite nor was there any indication of anything in the water before this incident. I instinctively yelled and kicked my legs to separate myself from the shark. I then saw the shark for the first time. The shark's mouth was open and I could see its teeth. I observed it from the side and it was withdrawing into the water after it bit me and let me go . . its body was somewhat curved toward me . . . The shark disappeared into the water and I never saw it again . . . This whole incident did not last longer than 2-3 seconds." The victim, bleeding profusely, then swam to shore, using his board and with some assistance from a nearby surfer. He suffered severe lacerations to both thighs, his left calf, and his right foot. He received emergency aid at the beach within 15 minutes and was then helicoptered to a nearby hospital. Radiographs demonstrated that the shark's teeth had penetrated to his femurs and other leg bones. There were no teeth or fragments left in the board or the victim. Other surfers in the water estimated the shark to be 16 ft long. We have no reason to doubt that the shark was a white shark. At the time of this writing, the victim is healing and despite some nerve damage will apparently regain the use of his limbs.
86. Deborah B. Franzman, swimmer; 19 August 2003; San Luis Obispo County, Avila Beach. Fatality. This account is based on RNL's examination of the victim at the San Luis Obispo County Coroner's Office, JMc's conversations with Jay Elder (Avila Beach Harbor Master), several media correspondents, and reports in the Los Angeles Times and the San Francisco Chronicle.

Franzman, a 50 -year-old athletic female Caucasian, swam most mornings along the offshore buoys 75 yds from shore south and east of the Avila Pier. On the morning of the attack she observed sea lions in the vicinity of a buoy in 18 ft of water and, wearing a black wet suit and fins, swam out to play with them. After swimming with the pinnipeds she began to swim back to the beach and was taken at 0820 by a large shark. A friend watching from shore observed the pinnipeds to scatter suddenly and "the swimmer was engulfed in a large breach of white water" (Los Angeles Times, 20 Aug. 2003). Her friend shouted for help and four lifeguards at the scene sprinted to her location, swam out and retrieved her, and began CPR. Paramedics from the California Division of Forestry soon arrived, but because their ambulance could not cross the beach sand, a lifeguard truck had to ferry the victim to the street where, on arrival, she was pronounced dead from massive blood loss resulting from her severed femoral artery. Radiographs were taken but no teeth or tooth fragments were found in the victim.

Later that day (ca. 1300) the crew of a local sportfishing boat (the Patriot) returned to the dock and observed a large shark chasing "seals" and jumping out of the water in the vicinity of the Avila Pier. Jay Elder reported that four days after the attack local fishermen had observed a large shark (reported to be 18 ft in length) take an adult harbor seal within 400 yds of the attack site. The fishermen related that three harbor seals leapt out of the water, followed by a shark that "came out of the water" and took the last seal by its fin, got it into its mouth, and took it under. This occurred due south of the south-flowing San Luis Obispo Creek, about 1200 ft from shore (water depth was 28 ft ). At that time, there had been a large shoal of anchovies and sardines in the area as well as a large increase in the number of harbor seals and sea lions (they counted 40 juvenile sea lions and 8-10 adult harbor seals within 0.5 mile of the attack site). We presume from the attacks upon the victim and the pinnipeds that the shark(s) involved was a white shark. Such a scenario involving increased fish prey being pursued by pinnipeds, which are in turn pursued by white sharks, is not uncommon in California, as well as in other parts of the world.

## In Oregon

Oregon 11. Rob MacKenzie, surfer; 21 September 1994; Tillamook County, Short Sand Beach. This account is based in part on Collier (2003), on an article in The Oregonian (22 September 1994), and on conversations with John Griffith.

Short Sand Beach is located in Oswald West State Park between Arch Cap and Manzanita, near Seaside in northern Oregon. MacKenzie, a 43-year-old male Caucasian, entered the ocean at ca. 1630 on a cloudless day. Sea conditions were calm, 1 m swell, and a light breeze, with water temperature at ca. $14^{\circ} \mathrm{C}$ and air temperate at $18^{\circ} \mathrm{C}$. He was 100 m from the shore above a sand and rock 4 m bottom. No pinnipeds were observed. He was using a 2 m yellow surfboard, and he and companion Greg Movsesyan had been surfing for 75 minutes when they observed a gray whale breaching about 1.6 km offshore. Collier (2003:146) reports that Movsesyan "noticed a gray form passing diagonally under my board which, because I had surfed often with dolphins in California didn't alarm me. The form approached Rob less than 15 ft away and, before I could say anything, it surfaced and bumped the side of Rob's board about three-quarters of the way forward. Rob went flying into the air, still attached to his board by a seven-foot leash, and came down in the water just in front of the shark. The board had become impaled sideways on the shark's lower jaw and, to dis-
lodge it, the shark raised its back half out of the water and slammed its head on the surface until the board floated free. Then the shark dived, getting its tail caught on the leash and pulling Rob and his board under as it swam for deeper water. Under the strain, the leash broke, shooting the board high in the air and allowing Rob to surface and retrieve it. We headed for shore, paddling until we reached waist-deep water. Rob had not been bitten and his wetsuit had only a graze-mark on the right hamstring, presumably from a shark tooth." Collier (2003) further reported that the underside of MacKenzie's board had been punctured by lower jaw teeth, forming a 35 cm wide arc. The midline of the arc, presumably the center of the shark's jaw, was located near the front of the board, about a third of the distance along its overall length.

Movsesyan stated (The Oregonian, 22 September 1994) that "the shark measured about 7 feet long from his dorsal fin to the fluke." The shark is presumed to have been a white shark, ca. 5 m in length.

0regon 12. John Forse, surfer; 21 April 1998; Lincoln County, Gleneden Beach State Park. This account is based primarily on our form returned by the victim, our conversations with J. Griffith, and Collier (2003).

Forse, a 50 -year-old male Caucasian, was using a 3 m black surfboard and wearing a black neoprene wetsuit and booties. He entered the water at about 0800 . The sea was calm, depth ca. 3-4 m, visibility ca. 2-3 m, and sea surface temperature ca. $12^{\circ} \mathrm{C}$ and air temperature ca. $18^{\circ} \mathrm{C}$. The seabed was sand with numerous sandbars. Forse had observed several seals close to shore prior to the attack. At 0930 he paddled out to four other surfers located ca. $100-150 \mathrm{~m}$ from shore. The five surfed together for about one hour and then the others returned to shore leaving Forse in the water alone. The victim reported that between 0930 and 1000 and 5 minutes before the attack he saw something break the surface of the water about 20 feet away, but he thought that it was a seal. As Forse was lying prone on his board, the shark bit the board and his upper right leg and pulled him beneath the surface. He reported that he was shaken underwater and then released and he surfaced, whereupon he saw a large white shark alongside himself, its dorsal fin an arm's length away. He then struck the shark's back ahead of its dorsal fin 4-5 times, and it then dove but pulled the board's ankle leash and Forse beneath the surface again. The leash then severed, the board erupted from beneath the sea surface, and Forse surfaced and swam 10 ft to his surfboard, then rode a wave and paddled with his arms to the beach. Forse's two friends on the beach had seen the attack and assisted him from shallow water to a vehicle and drove him to North Lincoln Hospital in Lincoln City. Emergency room physician Dr. Bruce Watanabe applied 50 stitches to the wounds, which consisted of 8 tooth punctures from $2.5-5 \mathrm{~cm}$ in length. The board experienced a 30 cm bite along its right side.

The attacking shark was a white shark, estimated by observers to be 4-5 m in length, which was corroborated by the tooth impressions left in the board. This is the first known white shark attack to have occurred in Lincoln County.

Oregon 13. Garry Turner, bodyboarder; 21 September 2002; Tillamook County, Cape Kiwanda. This account is based on conversations with J. Griffith and an AP wire story.

Turner, a 24-year-old male Caucasian, was bodyboarding with two friends ca. 60 m offshore at Cape Kiwanda. He was wearing fins and sitting on his board and talking with friends when something grabbed his left foot and pulled it strongly downward. Not immediately realizing that he had been bitten. he attempted to free his foot by kicking vigorously and pulling himself back onto his board. At this time the three surfers realized that a shark was involved. The shark appeared at the surface, headed again toward the surfers. and one of them yelled "shark, shark" as it submerged and disappeared. They then paddled quickly to shore. Turner was taken to Samaritan North Lincoln Hospital in Lincoln City and then by ambulance to Legacy Emmanuel Hospital in Portland. He suf-
fered deep wounds to the bones of his left ankle but did not have tendon damage.
Witnesses reported the shark to be "about eight feet long and seemed to lunge out of the water." The AP story reported that "area fishermen said it was likely a blue or a sand shark"; we find those identifications to be unlikely. Although the shark, as described, would be smaller than most attacking white sharks, we presume on the basis of the attacker's behavior that it was a white shark. This is the third reported shark incident at Cape Kiwanda. The two previous incidents, both involving surfers, occurred on 20 August 1983 (OR \#4, R. Weldon) and on 30 September 1984 (OR \#5, R. Rice); both involved white sharks and were non-injury encounters.

## Attacks Which We Do Not Consider To Have Been Provoked

A badly-wounded, naked corpse found floating 200 ft offshore from Sunset Cliffs, Point Loma, San Diego County, on 15 April 1994 was widely-reported to have been the result of an attack by a white shark. The body was later identified as that of Michelle Von Emster, a 25 -year-old Caucasian woman. Our investigation of this incident is based on JMc's conversations with R.H. Rosenblatt of the Scripps Institution of Oceanography and with N.D. Sperber of the San Diego County Medical Examiner's Office, and JMc's examination of 100 photographs taken of the corpse. Ms. Von Emster was of average height, slender, and weighed 59 kg . Both of her shoulders had been severely bitten, flesh had been removed from her left thigh, calf and buttocks, and her right leg was severed at midthigh and removed. Those injuries were indicative of partial consumption by sharks, either a white shark and/or blue sharks (Prionace glauca). As well, she had a broken neck, broken pelvis, a fractured rib, and three other bruised ribs. She was last seen alive the previous evening and could have been in the water as long as $16-18$ hours before she was found the following afternoon. The presence of sand and water in her lungs suggests that drowning was the cause of her death, and the apparent shark bites were subsequently inflicted. The extensive tissue damage appeared consistent with feeding by blue sharks. However, the removal of the right leg exposed much of the femur, and it lacked the scratches that one would expect from a feeding white shark or blue shark. The cliffside location where her personal belongings were found after her death, Sunset Cliffs, are dangerous and friable and about 25 m in elevation. Investigators have suggested (Matthews 1994) that her broken neck, pelvis and rib injuries, followed by her drowning, could have resulted from a fall from the cliff. Lacking evidence that would clearly indicate shark activity other than opportunistic scavenging upon a nearshore corpse, we do not consider this to be an unprovoked shark attack.

We also discount the purported attack by a shark upon Larry McCash while surfing at Sunset Cliffs, Point Loma, San Diego County, on 9 January 2001. Our knowledge of this incident is based on JMc's conversations with R.H. Rosenblatt of the Scripps Institution of Oceanography and newspaper articles in the San Diego Union Tribune (10 Jan. 2001, "Novice surfer claims shark attack") and the San Diego Peninsula Beacon (18 Jan. 2001, "Unconfirmed shark attack gnaws at skeptics"). Mr. McCash, 27, claims that while paddling toward shore a $6-8-\mathrm{ft}$ shark grabbed the tail of his surfboard (a 2 m split tail, twin skeg board) and pulled him back suddenly and violently. He claims to have struck the shark's snout three times with his fists. The shark was said by him to have a large, triangular-shaped dorsal fin and appeared to be entangled in a rope attached to a red-andwhite buoy. There were neither tooth fragments nor tooth marks left on his board. Mr. McCash was not injured and his hands were not abraded. We find the evidence inadequate to demonstrate that a shark attack had occurred.

On 23 September 1997 it was widely reported on San Francisco Bay Area television news programs that an unidentified male swimmer thought he was attacked by a shark while swimming across the Golden Gate. JMc spoke with the boat tender, Mr. George Roach, who had accompanied
the swimmer, and who saw a "fin" and said that the animal bumped the boat. The animal did not contact the swimmer. It was said to be 6 -ft long and its behavior, as described, was most likely that of a California sea lion.

We report the incident involving a shortfin mako (also called a bonito shark) (Isurus oxyrinchus) and a Southern California spearfisher on 28 August 1999, but do not consider it to have been an unprovoked attack. According to the San Diego Union newspaper (29 August 1999, pages B-1, B-3), Stewart Graham, 39, was freediving south of Coronado Island among kelp beds in approximately 30 ft of water when he observed a shark in the distance. The newspaper reported that ". . . when he dove under the surface again, he saw a large mako shark - its mouth wide open and sharp teeth shining - charging straight at him. With only a moment to think and the shark only about 15 ft away, Graham said, he grabbed the spear gun at his side - loaded with a thin, 6-foot metal spear - and aimed it at the fish's mouth. As the spear shot through the water, he said, the shark seemed to sense the danger and jerked its head to one side. The spear sank in the gills of the 10 -foot-long animal, which then passed Graham without touching him." The shark subsequently died, was taken to shore, and found to weigh 193 kg . To date, there is but one reported unprovoked attack on a human involving what was most likely a shortfin mako (Randall and Levy 1976), wherein a 20 -year-old menstruating woman was bitten approximately 12 times while swimming nearly 500 m offshore from Elat, Israel, in the northern end of the Red Sea. The shark, said to be 2 m in length, was not captured at the time, but the penetrations in her flesh indicated that it was a mako, and two days after the attack a $2.3-\mathrm{m}$ Isurus oxyrinchus was captured nearby. This then is the only report of an attack by what appears to be a shortfin mako; the purported attack of a "mako shark" on John Mark Regan at San Onofre, Orange County, on 29 November 1992, lacked any evidence or authenticity and has been discredited (McCosker and Lea 1996). In summary, although we do not discount that the mako shark might have attacked Mr. Graham (we are familiar with similar near-encounters by spearfishers with mako sharks, and none have resulted in attacks upon humans), we are not convinced that had Mr. Graham not acted as he did he would have been attacked.

And, finally, we relate the curious tale of Steve Rosenbloome, 33, who on 7 March 1994 was bitten by a 4 -ft lemon shark (Negaprion brevirostris) as he prepared to move the shark from its tank at the Shark Club Billiard Hall in Costa Mesa. The handler grabbed the shark's tail, it broke free, and bit him on the forearm. The wound required 100 stitches to close.

## Discussion

In our previous analysis of the biological and human aspects of white shark attacks (McCosker and Lea 1996:430-433), we attempted to identify and correlate factors responsible for the trends and patterns of attacks. The additional 20 unprovoked attacks in California and Oregon that we herein report have not significantly altered but have in fact reinforced our conclusions.

Those 20 attacks involved 18 men and 2 women; all were either teenagers or adults (age range $17-50$ years): victims comprised 11 surfers, 2 free divers, 1 commercial sea urchin diver, 3 bodyboarders, 1 scuba diver, 1 swimmer, and 1 windsurfer (Table 1). Two attacks were in southern California. 15 were in central and northern California, and 3 were in Oregon. All occurred at the surface except for that of the scuba diver (CA \#73. M. Flagg) who was being towed by an electric scooter. (The depth of the fatal attack upon CA \#71, J. Robinson, who was also using an electric scooter, is not known.) All wore black or black and blue neoprene wet suits. All victims, with two exceptions (CA \#73 scuba diver M. Flagg and CA \#76 abalone diver C. Tinley), did not see the shark prior to the attack. All known attacks occurred during daylight hours and were more prevalent at midday and in the afternoon (Fig. 3). Lacking comparable data for the time of day spent at

Table 1. Confirmed unprovoked attacks by Carcharodon carcharias upon humans in the eastern North Pacific. 1950-2003. Attacks at San Miguel Island are considered to be in "Central California." "Surface divers" includes scuba divers, breathhold divers, and a hookah diver who were attacked while at the surface. Note that in this and subsequent tables, the attacks on D. Webster and J. Greenlaw (2 Sept. 1974) and on T. McAllister and R. Stoddard (26 Jan. 1989) presumably, in each case, involved the same shark and each pairing is therefore counted as one.

|  | Swimmer | Surface <br> Divers | Surfer | Hookah | Scuba | Kayaker | Windsurfer | Bodyboarder |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Washington |  |  | 1 |  |  |  |  |  |
| Oregon |  |  | 12 |  |  |  |  | 1 |
| California |  |  |  |  |  |  |  |  |
| Central \& Northern | 6 | 32 | 23 | 6 | 5 | 3 | 1 | 2 |
| Southern |  |  |  |  |  | 2 |  |  |
| Guadalupe Island |  | 2 |  |  |  |  |  |  |
| Total ( $\mathrm{n}=95$ ) | 6 | 34 | 35 | 6 | 5 | 5 | 1 | 3 |
| Fatalities ( $\mathrm{n}=9$ ) | 4 | 3 | 1 |  |  | 1 |  |  |

risk by humans in the water, we are unable to draw any significant conclusions. Attacks occurred during April (1), May (1), June (2, representing the first NE Pacific attacks during June, if one discounts the 1959 attack on R. Pamperin), August (4), September (6), October (2), November (3), and December (1) (Table 2). As we previously reported, we found no correlation between seasonal timing and latitude or other factors, and again conclude that factors associated with human behavior most likely skew the preponderance of attacks during late summer. It is more likely that factors such as vacations, sea temperatures, and conditions that enhance recreational activities, and commercial sea urchin and sport abalone seasons, contribute to the likelihood of attacks. Human activity at the time of attack has not changed significantly, with surfers remaining as the primary victims (Table 1). A sailboarder and two bodyboarders were attacked for the first time in the ENP. This seems to reaffirm the hypothesis that those victims are also mistaken for pinnipeds by patrolling white sharks (for further discussion see Tricas and McCosker 1984; McCosker 1985; and McCosker and Lea 1996). And, despite the abundance of surfers, bodyboarders, sailboarders, and scuba divers in southern California, the absence of significant pinniped aggregations (with the exception of


Figure 3. Known time of attack (PST corrected for Daylight Savings in North Amc ... Charodon carcharias in the eastern North Pacific. $\mathrm{N}=87$.

Table 2. Monthly record of confirmed attacks by Carcharodon carcharias in the eastern North Pacific, 1950-2003.

| Month |  <br> Baja California |  <br> Washington | Total |
| :--- | :---: | :---: | ---: |
| January | 5 | 1 | 6 |
| February | 3 | 1 | 4 |
| March | 2 | 1 | 3 |
| April | 3 | 2 | 5 |
| May | 6 | 0 | 6 |
| June | 2 | 0 | 2 |
| July | 8 | 0 | 8 |
| August | 14 | 2 | 16 |
| September | 18 | 4 | 22 |
| October | 9 | 1 | 10 |
| November | 6 | 2 | 8 |
| December | 7 | 0 | 7 |

San Miguel Island and San Nicholas Island) and coastal river entrances (as occur in central and northern California, Oregon, and Washington) seems to explain the rarity of white shark encounters south of Point Conception (Table 3).

It is curious that a decreasing trend in attacks has occurred since 1991-1995 (Fig. 4). The historic high of 19 attacks during that period was followed by six in 1996-2000, and five in 2000-2003 (six attacks, which we do not include herein, occurred in 2004). It appears that recreational water use continues to rise in the NE Pacific, although we lack data to support this assumption. And, since the passage of California legislation in 1994 (AB 522), which prohibits the take of white sharks, it appears that their abundance is modestly increasing at some locations (see page 482 as concerns southern California sightings). We previously suggested, and remain convinced, that these discrepancies may be explained by: (a) humans having learned to avoid some locations where previous attacks have occurred with higher frequency, particularly the Farallon Islands, Tomales Point, and Año Nuevo Island, California; (b) educational programs which emphasize change in diver and swimmer behavior, such as avoidance of offshore exposed reefs and swimming among pinnipeds (CA \#84, D. Franzman, being an obvious example); and (c) spearfishermen being less likely to attach their catch to themselves.

The occurrence of an extreme El Niño (ENSO) event during 1997-1998 provided additional opportunity to evaluate the relationship of warm water conditions with white shark attacks. It has been suggested that white shark attacks are more frequent during ENSO events (three during the 1957-1959 ENSO and 4 during the 1982-1984 ENSO); however, only 3 attacks occurred during the 1997-1998 ENSO. In fact, the most extreme attack years in the NE Pacific (7 in 1974 and 5 in 1993) occurred during normal or cool oceanographic periods. We are unable to correlate an increase in attack occurrence with ENSO events.

A controversy involving the practice of attracting white sharks to caged sport divers using bait and blood ("chumming") within the Monterey Bay National Marine Sanctuary arose in 1993. A central California dive operator who had successfully attracted several white sharks near Año Nuevo Island met vociferous opposition from numerous surfing, diving, and conservation organizations who felt that chumming would endanger human water users (and, as a result, sharks as well). A decision was made in 1994 to prohibit chumming in central California waters in that it was illegal under the recently enacted white shark protection bill (AB 522). Fortunately, no shark/human encounters occurred at that time or in the vicinity of the chumming activity.

A remaining question concerning white shark encounters is the rarity of consumption of human victims. Consumption has occurred elsewhere (Martin 2003) but not to our knowledge in California, Oregon, or Washington among the victims that we have researched. However, three bod-
ies that we have reported on in previous papers have not been recovered. It is certainly possible that humans reported as "missing at sea" or "drowned but not recovered" in the NE Pacific might have been consumed by white sharks. We explain the low fatality rate in the NE Pacific (ca. $10 \%$ of victims), as compared to much higher rates (McCosker and Lea 1996) in Chile $(80 \%)$, Australia ( $62 \%$ ), and South Africa ( $24 \%$ ), by the nearly universal usage in the NE Pacific of the "buddy system," whereby a victim is taken to shore soon after attack, and where rapid transportation and expert medical


Figure 4. Confirmed attacks by Carcharodon carcharias in the eastern North Pacific, recorded in 5-year intervals. attention is generally available soon after the attack. And among the majority of the known fatalities, the victim died prior to or soon after being taken to shore. As well, we feel that the "bite and spit behavior" (Tricas and McCosker 1984; McCosker 1985; Martin 2003), employed by C. carcharias when attacking both pinniped and human victims, provides an opportunity for humans to survive if the initial attack does not kill the victim. We are unable to correlate defensive human behavior during and after the attack with the shark's behavior. Whereas several victims (e.g. CA \#70, 80, 81, 83, 84, and OR \#12) report to have struck the snout, jabbed the eye, grabbed the gills, fell upon, or kicked the shark, other victims did nothing and were also released. Hypotheses suggesting that human flesh and/or neoprene is distasteful to white sharks (not supported by evidence presented in Martin [2003], and elsewhere) and/or the bite-and-spit behavior is responsible for the temporary release of the victim, have yet to be convincingly proven.

We conclude our analysis of this last decade by reiterating our previous axiom (McCosker and Lea 1996:433), that "the potential for attack on humans by white sharks remains extremely low, and it is our hope that, by better understanding the behavior of Carcharodon carcharias, we can reduce this likelihood even further."

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## Literature Cited

Avderson, S.D., And K.J. Goldman. 1996. Photographic evidence of white shark movements in California waters. Bulletin of the California Department of Fish and Game 82:182-186.
A.vierson, S.D., and P. Pyle. 2003. A temporal, sex-specific occurrence pattern among white sharks at the South Farallon Islands, California. Bulletin of the California Department of Fish and Game 89:96-101.
Bonfil, R., M. Meyer, M.C. Scholl, R. Johnson, S. O’Brien, H. Oosthuizen, S. Swanson, D. Kotze and
M. Paterson. 2005. Transoceanic migration, spatial dynamics, and population linkages of white sharks. Science 310:100-106.
Boustany, A.M., S.F. Davis, P. Pyle, S.D. Anderson, B.J. Le Boeuf and B. Block. 2002. Expanded niche for white sharks. Nature 415:35-36.
Collier, R. 1964. Report on a recent shark attack off San Francisco, California. Bulletin of the California Department of Fish and Game 50:261-264.
Collier, R. 1992. Recurring attacks by white sharks on divers at two Pacific sites off Mexico and California. Environmental Biology of Fishes 33:319-325.
Collier, R. 1993. Shark attacks off the California islands: review and update. Pages 453-462 in F.G. Hochberg, ed., Third California Islands Symposium. Santa Barbara Museum of Natural History, Santa Barbara, California, USA. 661 pp.
Collier, R. 2003. Shark attacks of the twentieth century from the Pacific coast of North America. Scientia Publishing, Chatsworth, California, USA. 263 pp.
Davis, C. 1995. Shark attacks diver. The Monterey County Herald, 1 July 1995. pp. 1A, 4A.
Egaña, A.C., and J.E. McCosker. 1984. Attacks on divers by white sharks in Chile. Bulletin of the California Department of Fish and Game 70:173-179.
Ellis R.E., and J.E. McCosker. 1991. Great white shark. HarperCollins Publishers, New York, New York, USA. 270 pp .
Estes, J.A., B.B. Hatfield, K. Ralls, and J. Ames. 2003. Causes of mortality in California sea otters during periods of population growth and decline. Marine Mammal Science 91:198-216.
Follett, W.I. 1974. Attacks by the white shark, Carcharodon carcharias (Linnaeus), in northern California. Bulletin of the California Department of Fish and Game 60:192-198.
Goldman, K.J., and S.D. Anderson. 1999. Space utilization and swimming depth of white sharks, Carcharodon carcharias, at the South Farallon Islands, central California. Environmental Biology of Fishes 56:351-364.
Kelly, J.T., and A.P. Klimley. 2003. The occurrence of the white shark, Carcharodon carcharias, at the Point Reyes Headlands, California. Bulletin of the California Department of Fish and Game 89:187-196.
Klimley, A.P., And D.G. Ainley, eds. 1996. Great white sharks: The Biology of Carcharodon carcharias. Academic Press, San Diego, California, USA. 517 pp.
Klimley, A.P., B.J. Le Boeuf, K.M. Cantara, J.E. Richert, S.F.Davis, S.Van Sommeran, and J.T. Kelly. 2001. The hunting strategy of white sharks (Carcharodon carcharias) near a seal colony. Marine Biology 138:617-636.
Lea, R.N. 1987. Pacific coast shark attacks: What is the danger? Proceedings of the Conference: Sharks, An Inquiry into Biology, Behavior, Fisheries, and Use. Oregon State University Extension Service, Corvallis, Oregon, USA. 95 pp.
Lea, R.N.. and D.J. Miller. 1985. Shark attacks off the California and Oregon coasts: an update, 1980-84. Memoirs of the Southern California Academy of Sciences 9:136-150.
Martin. R.A. 2003. Field guide to the great white shark. ReefQuest Centre for Shark Research, spec. pub. 1. 185 pp .
Martin. R.A. 2005. Northerly distribution of white sharks, Carcharodon carcharias, in the eastern Pacific and relation to ENSO events. Marine Fisheries Review 66:16-26.
Martin. R.A., N. Hammerschlag. R.S. Collier and C. Fallows. 2005. Predatory behaviour of white sharks (Carcharodon carcharias) at Seal Island, South Africa. Journal of the Marine Biological Association of the U.K. 85:1121-1135.

Matthews, N. 1994. A great white? Or a great wrong? Exclusive Investigative report. Who killed Michelle Von Emster? Boating September 1994:112-116.
McCosker. J.E. 1981. Great white shark. Science 81 2:42-51.
MCCOSKER. J.E. 1985. White shark attack behavior: observations of and speculations about predator and prey strategies. Memoirs of the Southern California Academy of Sciences 9:123-135.
McCosker, J.E., A.vd R.N. Lea. 1996. White shark attacks in the eastern Pacific Ocean: an update and analysis. Pages $419-43+$ in A. P. Klimley and D. G. Ainley, eds., Great white sharks: The Biology of Carcharodon carcharias. Academic Press, San Diego, California, USA. 517 pp.

Miller, D.J., and R.S. Collier. 1981. Shark attacks in California and Oregon, 1926-1979. Bulletin of the California Department of Fish and Game 67:76-104.
Myrberg, A.A. 1978. Underwater sound - its effect on the behavior of sharks. Pages 391-417 in E.S. Hodgson and R.F. Mathewson, eds., Sensory Biology of Sharks, Skates, and Rays. Office of Naval Research, Arlington, Virginia, USA. 666 pp.
Pardini, A.T., C.S. Jones, L.R. Noble, B. Kreiser, H. Malcolm, B.D. Bruce, J.D. Stevens, G. Cliff, M.C. Scholl, M. Francis, C.A.J. Duffy, and A.P. Martin. 2001. Sex-biased dispersal of great white sharks. Nature 412:139-140.
Randall, J.E., and M.F. Levy. 1976. A near-fatal attack by a mako in the northern Red Sea. Israel Journal of Zoology 25:61-70.
Tricas, T.C., AND J.E. McCosker. 1984. Predatory behavior of the white shark (Carcharodon carcharias), with notes on its biology. Proceedings of the California Academy of Sciences, ser. 4, 43:221-238.

# A Revision of the Bavayia validiclavis group (Squamata: Gekkota: Diplodactylidae), a Clade of New Caledonian Geckos Exhibiting Microendemism 

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#### Abstract

The genus Bavayia as currently construed is paraphyletic relative to other New Caledonian diplodactylid geckos. Bavayia validiclavis, from the Massif du Panié in northeastern New Caledonia, is a relatively basal member of the entire New Caledonian diplodactylid radiation and is here recognized as the type species of a new genus characterized by small size and a unique combination of digital and coloration features. Recent surveys of the ultramafic massifs of northwestern New Caledonia have revealed seven additional species assignable to this genus. The new species are morphologically conservative but genetically distinctive from one another. Allopatric apecies occur on the Massif de Koniambo, Mt. Taom, Kaala, the Dôme de Tiébaghi and the adjacent Rivière Néhoué, and on the Îles Belep and Île Yandé, off the northern coast of the New Caledonian mainland. Two new species occur sympatrically on Sommet Poum, the northernmost of the mainland ultramafic massifs. Sequence data from the mitochondrial ND2 gene and the nuclear RAG-1 gene yield a single, well-supported phylogenetic hypothesis for the genus and suggest a time of 18.6-19.2 million years to common ancestry. The most recent speciation events in the genus are estimated to have occurred 5.7-10.1 million years ago. Cladogenesis within the genus may be associated with the erosion and fragmentation of ultramafic substrates and/or with climatic and vegetational changes in the region. Because of their very limited distributions, all of the new species are considered to be Endangered or Critically Endangered.


Key words: Gekkota, Diplodactylidae, Bavayia, Dierogekko gen. nov., species description, New Caledonia, molecular phylogeny, biogeography, conservation

The genus Bavayia was erected by Roux (1913) to accommodate two species (and three nonnominate subspecies) of New Caledonian geckos previously assigned to the widespread Pacific genus Lepidodactylus. Bavayia, along with two other endemic New Caledonian gecko genera, Rhacodactylus and Eurydactylodes, was subsequently referred to the endemic southwestern Pacific gekkotan subfamily Diplodactylinae (Underwood 1954, 1955; Kluge 1967, 1987; Russell and Bauer 2002), which has since been elevated to familial status (Good et al. 1997; Han et al. 2004). No taxonomic work on Bavayia was carried out for more than 70 years following the work of Roux (1913), but since the late 1980s, a series of contributions have raised Roux's subspecies to full

[^4]species (Sadlier 1989) and have identified seven additional taxa: B. septuiclavis, B. validiclavis, B. pulchella, B. exsuccida, B. geitaina, B. robusta, and B. madjo (Sadlier 1989; Bauer et al. 1998; Wright et al. 2000; Bauer et al. 2000). Previous phylogenetic analyses within the genus (Bauer 1990; Wright 1999) recognized two major intrageneric groupings, corresponding to the B. cyclura and $B$. sauvagii groups, diagnosable from one another on the basis of differences in digital morphology. Although some of the more recently described forms were referable to these groups (B. pulchella, B. exsuccida, B. geitaina in the B. sauvagii group and B. robusta in the B. cyclura group), the other taxa could not be so allocated and their affinities remained uncertain.

As part of ongoing studies of the New Caledonian herpetofauna, and especially in association with herpetofaunal surveys (2001-2002) of the Province Nord (Whitaker et al. 2004), we obtained Bavayia spp. from numerous, previously unsampled localities throughout northern New Caledonia. This material has been studied using traditional morpholoigical methods and through DNA sequencing. Initial results demonstrate that species diversity within Bavayia is much greater than previously appreciated. In particular, a number of new taxa have been discovered that are both similar in appearance and closely related to $B$. validiclavis.

Bavayia validiclavis was described by Sadlier (1989) on the basis of material from Mt. Panié. Until 2000 the only known areas of occurrence of this species were Mt. Panié and Mt. Mandjélia, two peaks in the northeast part of New Caledonia. It is a small species (to 45 mm SVL) and usually has a broad light brown to tan vertebral stripe covering most of the dorsal surface (although this is lacking in some specimens in which the dorsum is plain or has a series of light dashes along the dorsolateral margins). In addition, the claw of the first digit is offset and positioned asymmetrically within a groove in the apical lamella (a condition similar to that of the B. cyclura group), and males posses preanal pores in two rows, $12-16$ anteriorly and $8-11$ posteriorly. All new members of the $B$. validiclavis group share some of these features and may be collectively diagnosed from remaining Bavayia by them. In this paper we describe seven new species in this group and present a molecular phylogeny of this clade of northern New Caledonian endemic geckos.

A broad-scale phylogenetic analysis of all New Caledonian geckos (Bauer et al. 2004; Jackman et al. 2004; Jackman 2005) reveals that Bavayia as presently construed is paraphyletic, with the other endemic New Caledonian diplodactylids, Rhacodactylus and Eurydactylodes, being derived from within it. In order to retain only monophyletic genera we propose to recognize several genera within Bavayia sensu lato. The B. validiclavis group is a relatively basal member of the New Caledonian diplodactylid clade and is described herein as a new genus. This action causes minimal disruption to the established usage of generic names as the combination Bavayia validiclavis has received relatively little use, being applied only in the limited systematic literature dealing specifically with New Caledonian reptiles (see Bauer and Sadlier 2000).

## Material and Methods

Morphology. - The following measurements (to the nearest 0.1 mm ) were taken with DigiCal digital calipers: snout-vent length (SVL; from tip of snout to vent), trunk length (TrunkL; distance from axilla to groin measured from posterior edge of forelimb insertion to anterior edge of hindlimb insertion), crus length (CrusL: from base of heel to knee); tail length (TailL; from vent to tip of tail), tail width (TailW: measured at widest point of tail); head length (HeadL; distance between retroarticular process of jaw and snout-tip), head width (HeadW; maximum width of head), head height (HeadH: maximum height of head, from occiput to underside of jaws), ear length (EarL: longest dimension of ear): forearm length (ForeaL: from base of palm to elbow); orbital diameter (OrbD: greatest diameter of orbit), nares to eye distance (NarEye; distance between ante-
riormost point of eye and nostril), snout to eye distance (SnEye; distance between anteriormost point of eye and tip of snout), eye to ear distance (EyeEar; distance from anterior edge of ear opening to posterior corner of eye), internarial distance (Internar; distance between nares), and interorbital distance (Interorb; shortest distance between left and right supraciliary scale rows). Measurements and scale counts based on right side of animals unless otherwise noted.

Scale counts and external observations of morphology were made using a Nikon SMZ10 stereo dissecting microscope. Radiographs were prepared using a Faxitron closed cabinet x-ray unit. Specimens were x-rayed at $25-30 \mathrm{kV}$ for $25-30 \mathrm{sec}$ and imaged on Polaroid type 72 film. Photographs of preserved specimens were taken with a Nikon Coolpix 990 digital camera.

Comparisons were made with museum material in the collections of the California Academy of Sciences (CAS), the Australian Museum (AMS), and the Muséum National d'Histoire Naturelle, Paris (MNHN). Other collections mentioned are the Museum of Comparative Zoology, Harvard University (MCZ), Queensland Museum (QM), United States National Museum (USNM), and Yale Peabody Museum of Natural History (YPM).

Molecular Methods.- Genomic DNA was extracted using the Qiagen QIAmp tissue kit. PCR amplification was conducted under a variety of thermocyler parameters using a variety of primers (Table 1). Products were visualized via 1.5\% agarose gel electrophoresis. Amplified products were purified either using AmPure magnetic bead PCR purification kit or reamplified products were purified on $2.5 \%$ acrylamide gels (Maniatis et al. 1982) after being reamplified from $2.5 \%$ low melt agarose plugs. DNA from acrylamide gels was eluted from the acrylamide passively over two days with Maniatis elution buffer (Maniatis et al. 1982).

Cycle-sequencing reactions were performed using the Applied Biosystems BigDye ${ }^{\text {TM }}$ primer cycle sequencing ready reaction kit. The resulting products were purified using SeqClean magnetic bead purification kit. Purified sequencing reactions were analyzed on an ABI 3700 automated sequencer. To insure accuracy, negative controls were included in every reaction, complementary strands were sequenced, and sequences were manually aligned by eye using the original chromatograph data in the program SeqMan II. Sequences from all specimens of ingroup taxa sampled (Table 2) are available through GenBank

Phylogenetic Analyses.- Phylogenetic trees were estimated using parsimony, likelihood and Bayesian analysis. PAUP* 4.0b10a (Swofford 2002) was used to estimate parsimony and likelihood trees. Parsimony searches were conducted with 100 heuristic searches using random addition of sequences. Non-parametric bootstrap resampling was used to assess support for individual nodes using 1000 bootstrap replicates with ten random addition searches. For maximum likelihood analyses, ModelTest version 3.5 (Posada and Crandall 1998) was used to compare different models of sequence evolution with respect to the data. The chosen model was used to estimate parameters on the most parsimonious tree. These likelihood parameters were fixed and the most parsimonious trees were used as starting trees for branch swapping in 25 heuristic searches with random addition of taxa to find the overall best likelihood topology. To estimate a phylogenetic tree with a Bayesian framework MrBayes 3.0 (Huelsenbeck and Ronquist 2001) was used with the model chosen using ModelTest 3.5. The Bayesian analyses were initiated from random starting trees and run for $2,000,000$ generations with four incrementally heated Markov chains. Likelihood parameter values were estimated from the data and initiated using flat priors. Trees were sampled every 100 generations, resulting in 20,000 saved trees. To ensure that Bayesian analyses reach stationarity, the first 5000 saved trees were discarded as 'burn-in' samples.

Species Delimitation.- There has been much recent interest in the topic of species delimitation and its relationship to species concepts (Wiens and Servedio 2000; Brown and Diesmos 2001; Wiens and Penkrot 2002; Ferguson 2002; Hebert et al. 2003; Sites and Marshall 2003, 2004;

Blaxter 2004; Watson 2005). In this paper we follow a lineage-based species concept (Mayden 1997; de Queiroz 1998), but from a practical viewpoint, we are chiefly concerned with the properties that such lineages express that permit us to infer species boundaries (Otte and Endler 1989; Ereshefsky 1992; Howard and Berlocher 1998; Watson 2005). A variety of operational criteria for diagnosing species boundaries have been proposed (Sites and Marshall 2003, 2004). Wiens and Penkrot (2002) compared tree based approaches to species delimitation based on DNA data and both tree-based and character-based approaches based on morphological data. Although numerous studies have found congruence between character- and mtDNA tree-based approaches with respect to species boundaries (e.g., Hollingsworth 1998), Wiens and Penkrot (2002) found significant discordance in their analysis of Sceloporus. In such cases they favored the species limits suggested by mtDNA data, arguing that some taxa exhibit high levels of within species phenotypic variation and relatively low between species differentiation and that such circumstances represented a "worstcase scenario" for morphologically based species delimitation. In these cases haplotype differentiation may occur faster than change in diagnostic morphological characters, providing a more accurate picture of lineage boundaries.

The new genus described herein consists of putative taxa that differ very little with respect to most morphological characters. While, for pragmatic reasons, we would prefer to have a diversity of unambiguously diagnostic morphological features to support the recognition of each of the species level taxa we present herein, we accept that any data that identify independent lineages may be appropriately used in species delimitation. We have analyzed DNA sequence and characterbased species delimitations in light of each other. Subtle differences revealed by coloration and a few morphological features were in all cases corroborated by strong support from the gene trees. Although distribution patterns were not used in erecting our hypotheses of species boundaries, we considered geographic concordance (as reflected by allopatry) with both the tree- and characterbased species limits as indicative of lineage independence and, thus, supportive of our taxonomic decisions. Bergmann and Russell (2006) adopted a rather similar approach to the identification of species boundaries in the widespread Neotropical gecko Thecadactylus.

## Systematics

## Generic status of the Bavayia validiclavis group

Wright (1999) was the first to explicitly consider the phylogenetic position of Bavayia validiclavis in her allozyme-based analysis of the genus. She found B. validiclavis to form an unresolved trichotomy with other Bavavia and with Rhacodactylus. Thus, the distinctiveness of this taxon has been suspected for some time. As part of our molecular phylogenetic study of all New Caledonian lizards we included B. validiclavis as well as representatives of numerous isolated populations of validiclavis-like geckos collected chiefly in association with herpetofaunal surveys of the ultramafic peaks of the Province Nord (Whitaker et al. 2004).

On the basis of sequence data from the mitochondrial gene ND2 and the nuclear RAG-1 gene, we identified eight putative taxa among the validiclavis-like geckos studied. Together these form a well supported monophyletic group (posterior probability $=1.0$; bootstrap $=100 \%$ ) distinct from all other New Caledonian diplodactylids. The position of this group relative to other monophyletic units, however, is equivocal. In all analyses the group is retrieved in a basal polytomy with Bavayia madjo. all other Bavavia. and Rhacodactylus + Eurydactylodes, or it is very weakly supported as the sister group to all of these clades combined. There is no evidence that the validiclavis group is either embedded within Bavayia or the sister group to all other Bavayia exclusive of Rhacodactylus and Eurydactylodes.

As retention of the validiclavis group within Bavayia would render this genus paraphyletic, we recognize $B$. validiclavis and its close relatives as representatives of a new genus, Dierogekko, here proposed. As the only previously named species of this genus was described rather recently (Sadlier 1989), refers to a highly geographically restricted form, and has not been cited frequently in the literature (see Bauer and Sadlier 2000), this action may be accomplished with minimal disruption to familiar usage of the existing generic name Bavayia.

## Reptilia: Squamata: Diplodactylidae

Dierogekko Bauer, Jackman, Sadlier, and Whitaker, gen. nov.<br>Type Species: Dierogekko validiclavis (Sadlier, 1989).

Etymology.- Derived from the Greek dieros, meaning active or nimble and the Malay gekko. The name is masculine and refers to the nimble movements of members of this genus when foraging on vegetation at night.

Diagnosis.- Dierogekko, gen. nov. can be distinguished from all other diplodactylid geckos by the following combination of character states: body size small ( $<46 \mathrm{~mm} \mathrm{SVL}$ ); dorsal scalation granular, homogeneous; body without extensive skin webs or flaps; expanded subdigital lamellae under all toes; lamellae under penultimate phalanx of digits II-V of manus and pes paired or single; claw of digit I of manus and pes in a groove in the apical lamella between a larger medial scansor and a smaller lateral scansor; one or two (rarely three) internasal scales separating supranasal scales; lining of mouth unpigmented; dorsal pattern of longitudinal lines or series of spots or patternless, never with transverse markings; venter usually cream to light brown, sometimes pale yellow, never bright yellow.

Members of the genus Dierogekko superficially resemble members of the genera Bavayia and Oedodera, all of which are relatively small and predominantly brown in color. They differ from the recently described Oedodera (Bauer et al. 2006) in possessing divided distal subdigital lamellae (except $D$. poumensis) and in lacking a swollen neck and medial apical scansors on digit II of the pes. Dierogekko spp. may be distinguished from Bavayia sauvagii, B. ornata, and B. madjo by the position of the claw of digit I of manus and pes (in a groove between medial and lateral portions of a cleft apical scansor vs. lateral to a single medial apical scansor), from B. cyclura, B. montana, B. crassicollis, B. robusta, B. geitaina, and $B$. exsuccida by the absence of transverse dorsal markings and by much smaller body size ( $<50 \mathrm{~mm}$ vs. $>72 \mathrm{~mm}$ max. SVL) in all but the last of these species, and from B. pulchella and B. septuiclavis in having the entire dorsal surface lighter than the flanks and demarcated by a series of narrow, continuous or broken stripes (vs. a narrow pale vertebral stripe and/or no white border stripe).

Distribution.- Dierogekko is restricted to the northernmost areas of New Caledonia, from Île Pott in the Îles Belep, north of the Grande Terre (the main island of New Caledonia), to Mount Koniambio on the central west coast. On the east coast, the group reaches an apparent southern limit at Mt. Panié. All localities for species of Dierogekko lie within the Province Nord of New Caledonia.

Recognized Species.- Dierogekko validiclavis (Sadlier, 1989), D. thomaswhitei, sp. nov., D. poumensis, sp. nov., $D$. insularis, sp. nov., $D$. nehoueensis, sp. nov., D. kaalaensis, sp. nov., D. koniambo, sp. nov., and $D$. inexpectatus, sp. nov.

## Dierogekko validiclavis (Sadlier, 1989)

Figures 1-2.
Type material.- Holotype: Australian Museum (AMS) R77855, adult male, Mt. Panié (500-600 m elevation), Province Nord, New Caledonia, $20^{\circ} 33^{\prime} \mathrm{S}, 164^{\circ} 45^{\prime} \mathrm{E}$ [published coordinates], $20^{\circ} 33^{\prime} 43^{\prime \prime} \mathrm{S}$, $164^{\circ} 46^{\prime} 50^{\prime \prime}$ E [corrected coordinates], collected by R.A. Sadlier and P.R. Rankin, 17 December 1978. Paratypes: AMS R77847, 77853-54, 77856-58, 77895, 78353, same data as holotype; Queensland Museum (QM) J43980, Mandjélia near Pouébo, Province Nord, New Caledonia, $20^{\circ} 23^{\prime} \mathrm{S}, 164^{\circ} 33^{\prime} \mathrm{E}$; Muséum National d'Histoire Naturelle, Paris (MNHN) 1980.1067, Mt. Panié, Province Nord, New Caledonia.

Additional material. - AMS R144229-30, 149305, 149314, 149367-68, Mt. Panié, Province Nord, New Caledonia, $20^{\circ} 33^{\prime} 35^{\prime \prime}$ S, $164^{\circ} 47^{\prime} 03^{\prime \prime}$ E; AMS R 146350, CAS 198703-04, Mt. Mandjélia, Province Nord, New Caledonia, $20^{\circ} 24^{\prime} 15^{\prime \prime}$ S, $164^{\circ} 31^{\prime} 18^{\prime \prime}$ E; AMS R 153695-99, Mt. Mandjélia, Province Nord, New Caledonia, $20^{\circ} 24^{\prime} 17^{\prime \prime}$ S, $164^{\circ} 31^{\prime} 06^{\prime \prime}$ E.

Diagnosis.- Dierogekko validiclavis can be distinguished from all its congeners on the basis of the following combination of characters: size relatively large (to 45.0 mm ), one (rarely two) internasal scales; distal subdigital lamellae divided; male preanal pores in two rows ( $12-16$ in anterior row, 8-11 in posterior row). In addition, 27 presacral vertebrae (and concomitant reduction of pygal vertebrae to 4 rather than 5) have been recorded in a single specimen (CAS 198703), whereas this condition is not present in members of any other species examined, all of which have 26 presacral vertebrae. Narrow beige and dark brown stripes bordering dorsal pale region well-developed, beige stripe wider over sacrum and tail base than elsewhere.


Figure 1. Life photograph of a gravid female Dierogekko validiclavis with relatively weakly developed yellowish dorsal markings, from Mt. Panié, Province Nord, New Caledonia. Photo by R.A. Sadlier.


Figure 2. Life photograph of a male Dierogekko validiclavis with grayish-brown dorsal markings contrasting strongly from mid-brown flanks, from Mt. Panié, Province Nord, New Caledonia. Photo by R.A. Sadlier.

Description.- see Sadlier (1989).
Distribution and Natural History.- This species is the only member of its genus to occur on the east coast of the Grande Terre. It has been collected only on Mt. Panié (Taaluny) and Mt. Mandjélia (Tidiélic) (Fig. 3), but may be expected to occur in appropriate habitats of the Massif du Panié on Mt. Colnett (Bwa Yonâ) and Mt. Ignambi (Ngâbi), which lie between the two known localities. All known localities are at low- to mid-elevation, $400-500 \mathrm{~m}$. Specimens have been collected by day sheltering beneath rocks and logs in closed humid forest (Sadlier 1989) (Fig. 4). Dominant canopy species at this elevation include species of Anthocarapa, Archidendropsis, Calophyllum, Crossostylis, Cryptocarya, Cunonia, Dysoxylum, Ficus, Montrouziera, Neubergia, Pycnandra, Schefflera and Sy-ygium (Conservation International and Maruia Society 1998). These localities receive significantly more rainfall than do those of any of the other species in the genus (Sautter 1981). The herpetofauna of the Panié Massif is quite rich (Bauer and Sadlier 2000) and includes a number of other diplodactylids, including $B$. madjo as well as $B$. cf. montana and $B$. cf. cyclura (Bauer et al. 2000; Bauer and Sadlier 2000).

Conservation Status.- The Massif du Panié is one of the largest forested areas in New Caledonia and Mt. Panié itself is included in the Réserve Spéciale Botanique de Mt. Panié, which has had at least nominal protection since 1950 (Conservation International and Maruia Society


Figure 3. Landsat 7 image of the northern portion of the Province Nord, New Caledonia, showing the collection localities of the eight species of Dierogekko. Key: orange $=$ D. validiclavis, dark green $=D$. . oniambo, light green $=D$. kaalaensis, blue $=D$. thomaswhitei, purple $=D$. nehoueensis, red $=D$. insularis, black $=D$. poumensis, yellow $=D$. inexpectatus. Image from the Millenium Coral Reef Landsat Archive.
1998). Mt. Panié itself has never been populated and more than 32,500 ha of rainforest remain on the massif (Jaffré et al. 1998). It is widely regarded as one of the most critical conservation areas in New Caledonia (Conservation International and Maruia Society 1998; Ekstrom et al. 2000). Dierogekko validiclavis may be potentially at risk from agricultural clearing and burning at low elevation on the east coast of New Caledonia and from mid-elevation timber extraction on Mt. Mandjélia, as well as from introduced fire ants, which are locally abundant at low elevation on Mt. Panié, rats and cats. However, most of these threats


Figure 4. Forested habitat of Dierogekko validiclavis on the slopes of the Massif du Panié, Province Nord, New Caledonia. Photo A.M. Bauer. affect only the forest edge and the core closed forest habitat of this species is generally well protected. On this basis D. validiclavis is regarded as Vulnerable (Sadlier and Bauer 2003).

## Dierogekko koniambo Bauer, Jackman, Sadlier, and Whitaker, sp. nov.

Figures 5-6.
Type Material.- Holotype: MNHN 2004.0016 (formerly AMS R 161128): Adult male; New Caledonia, Province Nord, Massif de Koniambo, 8 km NE Koné, headwaters of Rivière Pandanus, $20^{\circ} 59^{\prime} 42.5^{\prime \prime} \mathrm{S}, 164^{\circ} 48^{\prime} 56.0^{\prime \prime} \mathrm{E}$ (elevation 800 m ), collected by A.H. Whitaker and V.A. Whitaker, 7 June 2002. Paratypes: AMS R 161114, 161130, CAS 231874-75: Adult males; AMS R 161131, CAS 231873: Adult females; New Caledonia, Province Nord, Massif de Koniambo, 8 km NE Koné, headwaters of Rivière Pandanus, $20^{\circ} 59^{\prime} 42.5^{\prime \prime} \mathrm{S}, 164^{\circ} 48^{\prime} 56.0^{\prime \prime} \mathrm{E}$ (elevation 850 m ), collected by A.H. Whitaker and V.A. Whitaker, 6 June 2002.

Etymology.- The species name koniambo is a noun in apposition and refers to the ultramafic massif (maximum elevation 940 m ) to which this species appears restricted.

Diagnosis.- Dierogekko koniambo can be distinguished from all congeners on the basis of the following combination of characters: size intermediate (to 43.0 mm SVL ), 1-2 (rarely three) internasal scales; distal subdigital lamellae divided; male preanal pores in a single row of 10-12. Narrow beige and dark brown stripes bordering pale dorsal region weakly developed, sometimes absent, on body between nape and sacrum.

Description (based on holotype).- Adult male. SVL 42.6 mm ; TailL 40.8 mm (distal 23.5 mm regenerated). Head moderately long (HeadL/SVL ratio 0.29), relatively narrow (HeadW/HeadL ratio 0.59), somewhat depressed (HeadH/HeadL ratio 0.41), set off from relatively thick neck. Loreal region without inflated canthal area; interorbital region slightly depressed. Snout moderately elongate (SnEye/HeadL ratio 0.40), blunt; longer than eye diameter (OrbD/SnEye ratio $0.64)$; scales on snout and forehead small, rounded, granular to weakly conical, homogeneous; scales on snout much larger than those on occipital region. Eye relatively large (OrbD/HeadL ratio 0.25 ); pupil vertical with crenelated margins; supraciliaries short, bearing $1-3$ elongate spines near posterodorsal margin of orbit. Ear opening oval, angled posterodorsally at an angle of $45^{\circ}$ from horizontal, relatively large (EarL/HeadL ratio 0.12); eye to ear distance subequal to diameter of eyes (EyeEar/OrbD ratio 1.02 ). Rostral wider ( 1.6 mm ) than deep ( 1.2 mm ), incompletely divided dorsally. Two moderately enlarged supranasals separated by three hexagonal internasals in a single transverse row. Rostral in contact with first supralabials, nostrils, supranasals and all three internasals. Nostrils rounded, each surrounded by supranasal, rostral, first supralabial, nasal and two postnasals. At least four rows of small scales separate orbit from supralabials. Mental triangular, approximately as wide ( 1.2 mm ) as deep ( 1.2 mm ). A single enlarged ( $15-20$ times size of granular throat scales) hexagonal postmental, anterior apex narrowest, bordered by mental, first infralabials, and five enlarged chin shields, three posteriorly and one each posterolaterally. Two to three scale rows posterior to postmental and medial to infralabials enlarged relative to remainder of chin and throat scales. Supralabials to midorbital position 7/6; total enlarged supralabials 9/7; supralabial scales to angle of jaws 12/11. Enlarged infralabials 9/7; infralabials to angle of jaws 12/11. Interorbital scale rows across narrowest point of frontal bone 17.

Body slender, elongate (TrunkL/SVL ratio 0.43); no ventrolateral folds. Dorsal scales smooth, granular. homogeneous. Ventral scales larger than dorsals, smooth, hexagonal and subimbricate to imbricate, roughly uniform in size across venter. Approximately 124 scale rows around midbody. Gular region with homogeneous, smooth granular scales, equivalent in size to dorsal granules.

No enlarged precloacal or femoral scales; precloacal pores relatively small, in single angled series of 10 , with a single poreless scale separating left and right pores; no femoral pores. 2(L)-3(R) enlarged, smooth, conical cloacal spurs.

Scales on palm and sole smooth. rounded. Scalation on dorsal surfaces of limbs similar to body dorsum. Fore and hindlimbs short and thick (ForeaL/SVL ratio 0.11; CrusL/SVL ratio 0.14). Digits


Figure 5. Holotype of Dierogekko koniambo (MNHN 2004.0016 ) from the Massif de Koniambo, Province Nord, New Caledonia. Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.


Figure 6. Life photograph of the holotype of Dierogekko koniambo (MNHN 2004.0016). Photo by A.H. Whitaker.
moderately dilated; claws well developed and recurved on digits II-V; claw much reduced and less strongly recurved on digit I, situated between asymmetrical distal pads (lateral pad approximately twice size of medial). Basal subdigital lamellae broad, rectangular, becoming bowed distally and angled and divided beneath distal phalanges (except terminal scansor). Scansors (terminal scansors of digit I not included in counts): 4-8-11-11-9 manus; 6-9-12-13-12 pes. Relative length of digits: $\mathrm{IV}>\mathrm{III}>\mathrm{II}>\mathrm{V}>\mathrm{I}$ (manus); $\mathrm{IV}>\mathrm{III} \sim \mathrm{V}>\mathrm{II}>\mathrm{I}$ (pes); interdigital webbing weakly developed between all digits of manus and digits I-IV of pes, absent between digits IV and V of pes. Regenerated tail approximately equal to body length (TailL/SVL ratio 0.96 ), thick, slightly constricted at base, tapering gradually along distal $1 / 3$. No caudal tubercles; dorsal caudal scales subconical basally, becoming flatter distally, pentagonal with free margins rounded, juxtaposed to subimbricate, eight rows per tail segment; subcaudal scales approximately 1.5 times larger than dorsals.

Osteology: Parietal bones paired; stapes imperforate. Phalangeal formula 2-3-4-5-3 for manus and 2-3-4-5-4 for pes. Presacral vertebrae 26, including 3 anterior cervical (without ribs), 1 lumbar, and 2 sacral vertebrae; 5 pygal and 5.5 post pygal caudal vertebrae anterior to regenerate region in tail of holotype ( 6.5 post pygal vertebrae to point of regeneration in longest-tailed paratype, CAS 231875). Holotype and male paratypes with one pair of crescentic cloacal bones at the level of second to third pygal vertebrae. Endolymphatic sacs not enlarged extracranially.

Coloration (in preservative): Dorsal ground color mid- to dark brown, with a broad median region of paler grayish-brown extending from top of head onto tail, edged on each side by two incomplete and diffuse stripes, the inner beige and outer dark brown; stripes most prominent on nape and over lumbar and sacral regions; stripes discrete on sacrum, but becoming more diffuse on tail base, with dark stripe fading entirely and light stripe expanding and fusing with that of opposite side to form a series of cream to beige blotches on dorsum of original tail. Area from nostril through ventral half of orbit to above ear opening darker than adjacent surfaces. Labial scales midto dark brown with cream spots within scales or bracketing sutures. Iris coppery with brownish reticulations. Flanks mid-brown. Limbs uniform brown; palms, soles and subdigital surfaces brown to grayish-brown. Dorsum of regenerated portion of tail midbrown with irregular darker markings. Venter beige with extensive brown flecks on most scales, especially laterally and under limbs. Chin and throat brown with a large oval central spot free of pigment. Venter of original portion of tail mottled light brown; venter of regenerate grayish-brown.

Variation.- Comparative mensural data for the holotype and paratypes are given in Table 3. Meristic characters of paratypes are mostly similar to those of the holotype, and are mentioned hereafter if they differ. Only one (AMS R 161114, 161130-31) or two (CAS 231873-75) internasals in paratypes. Precloacal pores in single row of 10 (CAS 231874), 11 (AMS R 161130), or 12 (AMS R 161114, CAS 231875) in male paratypes, absent in females. Precloacal pores in continuous series (AMS R 161130, CAS 231875), or with one (AMS R 161114) or three (CAS 231874) poreless
scales between left and right series.
Dorsum more-or-less uniform yellowish-brown with dorsal stripes absent except for some trace on sacrum and nape only in AMS R 161114 and 161131. Vertebral region yellowish-brown with bordering stripes variably developed, contrasting with greyish brown dorsolateral and lateral surfaces in AMS R 161129 and CAS 231875. CAS 231874 intermediate in pattern boldness between holotype and CAS 231873 . AMS R 161130 similar to holotype but with light stripes bordering vertebral region more prominent. Throat heavily mottled with brown in AMS R 161130 and CAS 231874-75, less strongly pigmented in CAS 231873 and AMS R 161131 and very faintly pigmented in AMS R 161114. All paratypes lack the oval pigmentless gular patch of the holotype.

Distribution and Natural History. - This species is known only from the Massif de Koniambo, an ultramafic peak (maximum 940 m elevation) in the northwestern Grande Terre (Fig. 3). The vegetation of Koniambo was discussed by Jaffré (1974). Specimens were collected in montane closed forest on the summit plateau. The species was also observed in maquis at mid-elevation ( $500-600 \mathrm{~m}$ ). Seven mites (probably Trombiculidae) were located on one specimen (AMS R 161129), three around margin of right eye, one attached to the margin of the left eye, and one each anterior to the insertion of the left forelimb, in the left axillary "pocket," and above the right forelimb insertion.

Other reptiles collected at or near the type locality include Bavayia aff. montana, Eurydactylodes vieillardi, Rhacodactylus auriculatus, Caledoniscincus austrocaledonicus, C. atropunctatus, Lioscincus nigrofasciolatus, Marmorosphax tricolor, and Tropidoscincus boreus (Whitaker et al. 2004).

Conservation Status.- Dierogekko koniambo was abundant at its type locality in 2002, with as many as 15 individuals occupying a single small tree and was also abundant in maquis at lower elevation (Whitaker et al. 2004). However, it is at risk from several threats. Introduced mammals including Rattus rattus, R. exulans, and feral cats occur on Koniambo and are potential predators. In addition deer (Cervus timorensis) and feral pigs are also present and may be expected to degrade the vegetation. More significantly, the Massif de Koniambo is being developed as a major nickel mine, thus placing the only known locality for this gecko at grave risk. On this basis we regard the species as Critically Endangered.

## Dierogekko kaalaensis Bauer, Jackman, Sadier, and Whitaker, sp. nov.

Figures 7-8.
Type Material.- Holotype: MNHN 2004.0017 (formerly AMS R 161096): Adult male; New Caledonia, Province Nord, Kaala massif, headwaters of Oué Injob, 6 km N Kaala-Gomen, 20웅́03.2"S, $164^{\circ} 22^{\prime} 49.0^{\prime \prime}$ E (elevation 900 m ), collected by A.H. Whitaker and V.A. Whitaker, 2 June 2002. Paratypes: AMS R 161098, CAS 231870: Adult males: AMS R161097, CAS 231871: Adult females; collection data as for holotype. CAS 231872: Adult female; New Caledonia, Province Nord, Kaala massif, east side Piton de Pandop, 9 km SE Koumac. $20^{\circ} 35^{\prime} 16.5^{\prime \prime} \mathrm{S}, 164^{\circ} 22^{\prime} 04.6^{\prime \prime} \mathrm{E}$ (elevation 500 m ), collected by A.H. Whitaker and V.A. Whitaker, 3 June 2002.

Etymology. - The specific epithet kaalaensis is derived from the Kaala massif, the ultramafic mountain ( 1079 m maximum elevation) to which this species appears restricted.

Diagnosis.- Dierogekko kaalaensis can be distinguished from all congeners on the basis of the following combination of characters: size relatively large (to 45.4 mm SVL), 1-2 internasal scales; distal subdigital lamellae divided; male preanal pores in a single row of 12-15. Narrow dark brown markings bordering dorsal pale region laterally reduced to a series of widely spaced dark speckles corresponding to individual granular scales.

Description (based on holotype).- Adult male. SVL 42.2 mm ; TailL 41.8 mm (distal 30.4
mm regenerated). Head relatively short (HeadL/SVL ratio 0.27) and wide (HeadW/ HeadL ratio 0.70), depressed (HeadH/HeadL ratio 0.34 ), weakly set off from relatively thick neck. Loreal region without inflated canthal area; interorbital region slightly depressed. Snout moderately short (SnEye/HeadL ratio 0.37 ), blunt; longer than eye diameter (OrbD/SnEye ratio 0.60); scales on snout and forehead small, rounded, granular to weakly conical, homogeneous; scales on snout much larger than those on occipital region. Eye moderately large (OrbD/HeadL ratio 0.22 ); pupil vertical with crenelated margins; supraciliaries short, bearing $1-3$ elongate spines near posterodorsal margin of orbit. Ear opening oval, angled posterodorsally at an angle of $45^{\circ}$ from horizontal, relatively large (EarL/HeadL ratio $0.14)$; eye to ear distance greater than diameter of eyes (EyeEar/OrbD ratio 1.16). Rostral much wider ( 2.3 mm ) than deep ( 1.3 mm ), incompletely divided dorsally. Two moderately enlarged supranasals separated by one large hexagonal internasal. Rostral in contact with first supralabials, nostrils, supranasals and internasal. Nostrils rounded, each surrounded by supranasal, rostral, first supralabial, nasal and two postnasals. At least four rows of small scales separate orbit from supralabials. Mental triangular, wider ( 1.9 mm ) than deep ( 1.2 mm ). A single enlarged ( $15-20$ times size of granular throat scales) irregular, octagonal postmental, anterior and posterior apices narrowest, bordered by mental, first infralabials, and five enlarged chin shields, three posteriorly and one each posterolaterally. Two to three scale rows posterior to postmental and medial to infralabials enlarged relative to remainder of chin and throat scales. Supralabials to midorbital position 7/8; total enlarged supralabials $10 / 11$; supralabial scales to angle of jaws $13 / 15$. Enlarged infralabials $9 / 8$; infralabials to angle of jaws 13/12. Interorbital scale rows across narrowest point of frontal bone 15 .

Body slender, moderately elongate (TrunkL/SVL ratio 0.38); no ventrolateral folds. Dorsal scales smooth, granular, homogeneous. Ventral scales larger than dorsals, smooth, with rounded free margins, subimbricate to imbricate, roughly uniform in size across venter. Approximately 129 scale rows around midbody. Gular region with homogeneous, smooth granular scales, equivalent in size to dorsal granules.

No enlarged precloacal or femoral scales; precloacal pores relatively small, in single angled series of 12 , with a single poreless scale separating left and right pores; no femoral pores. Two enlarged, smooth, conical, somewhat laterally projecting cloacal spurs, posteroventral spur larger.

Scales on palm and sole smooth, rounded. Scalation on dorsal surfaces of limbs similar to body dorsum. Fore and hindlimbs short and thick (ForeaL/SVL ratio 0.13; CrusL/SVL ratio 0.15). Digits moderately dilated; claws well developed and recurved on digits II-V; claw much reduced and less
strongly recurved on digit I, situated between asymmetrical distal pads (lateral pad approximately twice size of medial). Basal subdigital lamellae broad, rectangular, becoming bowed distally and angled and divided beneath distal phalanges (except terminal scansor). Scansors (terminal scansors of digit I not included in counts): 5-8-11-12-12 manus; 5-10-12-13-12 pes. Relative length of digits: IV $>$ III $>\mathrm{II}>\mathrm{V}>$ I (manus); IV $>$ III $\sim \mathrm{V}>\mathrm{II}>\mathrm{I}$ (pes); interdigital webbing weakly developed between all digits of manus and digits I-IV of pes, absent between digits IV and V of pes. Regenerated tail approximately equal to body length (TailL/SVL ratio 0.99 ), thick, slightly constricted at base, tapering gradually along distal $1 / 3$. No caudal tubercles; dorsal caudal scales squarish to oval, juxtaposed to subimbricate, eight rows per tail segment; subcaudal scales approximately 1.5 times larger than dorsals, more strongly imbricating.

Osteology: Parietal bones paired; stapes imperforate. Phalangeal formula 2-3-4-5-3 for manus and 2-3-4-5-4 for pes. Presacral vertebrae 26, including 3 anterior cervical (without ribs), 1 lumbar, and 2 sacral vertebrae; 5 pygal and 3.5 post pygal caudal vertebrae proximal to regenerated portion of tail ( 17.5 post pygal vertebrae to point of regeneration in paratype with longest tail, CAS 231870). Holotypes and male paratypes with one pair of crescentic cloacal bones present at level of second to third pygal vertebrae. Endolymphatic sacs not enlarged extracranially. In the juvenile specimen, CAS 231871, the epiphyses of the long bones remain unfused.

Coloration (in preservative): Dorsal ground color uniform medium brown, with single dark brown granular scales scattered on dorsum, especially in two parallel parasagittal longitudinal lines, each consisting of about 10 widely spaced dark granular scales. A pair of very faint, but more continuous longitudinal markings on pygal portion of tail, each consisting of a more medial beige stripe and a more lateral dark brown line, each about three granular scales in width, becoming fainter and more sinuous on original postpygal portion of tail. Regenerated portion of tail medium brown with irregularly scattered dark brown scales. Snout uniform medium brown, sides of neck with some mottling. Labials dark brown with cream (pigmentless) spots. Iris coppery with brownish reticulations. Flanks somewhat paler than dorsum and slightly mottled. Limbs similar to dorsum; palms, soles and subdigital surfaces brown to grayish-brown. Venter beige with many brown flecks on individual scales, pigmentation heaviest under limbs, around cloaca and on mottled chin and throat. Venter of both original and regenerated portions of tail grayish-brown with scattered darker brown scales.

Variation.- Comparative mensural data for the holotype and paratypes are given in Table 4. Meristic characters of paratypes are mostly similar to those of the holotype, and are mentioned hereafter if they differ. Mostly original tail of CAS 231870 is $118 \%$ of SVL. Two internasal scales in all paratypes except CAS 231871. All paratypes with only two scales bordering enlarged postmental posteriorly. Number and size of enlarged supraciliary scales highly variable across type series. Precloacal pores in male paratypes in a single series of 8 (left) and (7) right, separated by one poreless scale (CAS 231870) or in a continuous series of 13 (AMS R 161098).

Distinctness of middorsal stripe variable. Most specimens with stripe distinctly more yellow-ish-brown than remainder of dorsum and flanks more grayish-brown than in holotype (e.g. AMS R 161097-98, CAS 231872). Borders of middorsal stripe always more well defined on lumbar and sacral regions and on nape. Borders consisting of small scattered dark markings in AMS R 161097-98. CAS 231871, more-or-less complete lateral dark lines and incomplete medial beige lines in CAS 231870, and incomplete beige lines with very narrow dark brown lateral borders in CAS 231872. Top of head generally same color as middorsal stripe, either uniform (AMS R 161097, CAS 231872) or with dark speckling (AMS R 161098) or heavier patterning with larger dark markings continuing on to snout (CAS 231871). Original tail of CAS 231870 boldly patterned with contiguous light brown blotches with dark brown borders. Degree of ventral pigmentation
comparable to holotype except in CAS 231872, which is distinctly paler.

Distribution and Natural History.This species is known only from the Kaala massif, an ultramafic peak ( 1079 m maximum elevation) in the northwestern Grande Terre (Fig. 3). The vegetation of Kaala was discussed by Virot (1956). Piton de Pandop ( 823 m ) is the northernmost peak in the Kaala massif, lying north of the Oué Tenguoa catchment. The specimens from the headwaters of Oué Injob were collected on small shrubs in maquis vegetation (Fig. 9), while that from Piton de Pandop was in closed forest. This species has also been found in riparian forest in the lower reaches of the Oué Injob ( 80 m elevation).

Other reptiles collected at the headwaters of the Oué Injob include Eurydactylodes agricolae, Rhacodactylus auriculatus, Caledoniscincus atropunctatus, Marmorosphax aff. tricolor, and Tropidoscincus boreus. In addition, Bavayia aff. cyclura and Lioscincus nigrofasciolatus have been collected at the paratype locality at Piton de Pandop, and at the low elevation site Hemidactylus frenatus, Oedodera marmorata, and an undescribed member of the Bavayia cyclura complex are present.

## Conservation Status. - Dierogekko

 kaalaensis is known only from three localities on the Kaala massif. The area supports introduced Rattus species, cats, deer and pigs and has been heavily exploited by mining. Two mines on the summit of the massif are still active and there are current plans to re-open one of the old mines on the western slopes. In addition, recent wildfires have severely affected the western slopes of Kaala. As this species is at potential risk from several threats in its restricted range, we regard it as Critically Endangered.
## Dierogekko thomaswhitei Bauer, Jackman, Sadlier, and Whitaker, sp. nov.

Figures 10-12.
Type Material.- Holotype: MNHN 2004.0016: Adult male; New Caledonia, Province Nord, Massif d'Ouazangou-Taom, Mt. Taom, vicinity Gomen Mine, $20^{\circ} 46^{\prime} 40^{\prime \prime} \mathrm{S}, 164^{\circ} 34^{\prime} 38^{\prime \prime} \mathrm{E}$ (elevation 870 m ), collected by R.A. Sadlier, T. Jackman and G. Watkins-Colwell, 23 January 2003. Paratypes: CAS 231837, AMS R 166975: Adult males; CAS 231838; Juvenile female; same collection data as holotype. AMS R 161153, 161178, CAS 231877: Adult males; AMS R 161180, CAS 231876,: Adult females; New Caledonia, Province Nord, Massif d'Ouazangou-Taom, Mt. Taom, Gomen Mine, 12 km NE Ouaco, Province Nord, New Caledonia, $20^{\circ} 46^{\prime} 36.0^{\prime \prime} \mathrm{S}, 164^{\circ} 33^{\prime} 44.9^{\prime \prime} \mathrm{E}$ (elevation 850 m ), collected by A.H. Whitaker and V.A. Whitaker, 11 June 2002.

Etymology.- The specific epithet is a patronym honoring Dr. Thomas White, through whose generosity the automated sequencer used in our molecular phylogenetic analyses of the New

Caledonian lizard fauna was obtained. The name is masculine and is formed in the genitive singular.

Diagnosis.- Dierogekko thomaswhitei can be distinguished from all congeners on the basis of the following combination of characters: size relatively large (to 44.9 mm SVL), 1 internasal scale; distal subdigital lamellae divided; male preanal pores in two rows (12-14 in anterior row, 1-5 in posterior row). Narrow beige and dark brown longitudinal stripes vague, cream markings coalesce over forelimb insertion, sacrum, and tail base; dorsal surface of head darker than lateral.

Description (based on holotype).— Adult male. SVL 41.7 mm ; TailL 39.0 mm (distal 23.4 mm regenerated). Head relatively short (HeadL/SVL ratio 0.30), relatively narrow (HeadW/HeadL ratio 0.63 ), moderately depressed (HeadH/HeadL ratio 0.38 ), set off from relatively thick neck. Loreal region without inflated canthal area; interorbital region slightly depressed. Snout short (SnEye/HeadL ratio 0.33), blunt; longer than eye diameter (OrbD/SnEye ratio 0.68); scales on snout and forehead small, rounded, granular to weakly conical, homogeneous; scales on snout larger than those on occipital region. Eye moderately large (OrbD/HeadL ratio 0.23); pupil vertical with crenelated margins; supraciliaries short, bearing 1-3 elongate spines near posterodorsal margin of orbit. Ear opening oval, angled posterodorsally at an angle of $45^{\circ}$ from horizontal, relatively large (EarL/HeadL ratio 0.13); eye to ear distance slightly greater than diameter of eyes (EyeEar/OrbD ratio 1.05 ). Rostral much wider ( 2.1 mm ) than deep ( 1.1 mm ), incompletely divided dorsally. Two moderately enlarged supranasals separated by one large internasal, approximately same size as supranasals. Rostral in contact with first supralabials, nostrils, supranasals and internasal. Nostrils rounded, each surrounded by supranasal, rostral, first supralabial, nasal and two postnasals. At least four rows of small scales separate orbit from supralabials. Mental triangular, wider ( 1.1 mm ) than deep ( 0.9 mm ). A single enlarged (approximately 12 times size of granular throat scales) irregular, heptagonal postmental, anterior and posterior apices narrowest, bordered by mental, first infralabials, and five enlarged chin shields, three posteriorly and one each posterolaterally. Two to three scale rows posterior to postmental and medial to infralabials enalrged relative to remainder of chin and throat scales. Supralabials to midorbital position $8 / 9$; total enlarged supralabials $10 / 10$; supralabial scales to angle of jaws 13/14. Enlarged infralabials 9/10; infralabials to angle of jaws 12/13. Interorbital scale rows across narrowest point of frontal bone 16.

Body slender, moderately elongate (TrunkL/SVL ratio 0.38); no ventrolateral folds. Dorsal scales smooth, granular, homogeneous. Ventral scales larger than dorsals, smooth, with rounded free margins, subimbricate to imbricate, roughly uniform in size across venter. Approximately 121 scale rows around midbody. Gular region with homogeneous, smooth granular scales, equivalent in size to dorsal granules.

No enlarged precloacal or femoral scales; precloacal pores relatively small, in two angled series in adjacent scale rows, anterior continuous row of 13 pores, posterior row of one pored scale (left) separated by five poreless scales from two pores on right side. Two enlarged, smooth, conical, somewhat laterally projecting cloacal spurs, anterodorsal spur larger.

Scales on palm and sole smooth, rounded. Scalation on dorsal surfaces of limbs similar to body dorsum. Fore and hindlimbs short and thick (ForeaL/SVL ratio 0.13; CrusL/SVL ratio 0.14). Digits moderately dilated; claws well developed and recurved on digits II-V; claw much reduced and less strongly recurved on digit I, situated between asymmetrical distal pads (lateral pad approximately 1.5 times size of medial). Basal subdigital lamellae broad, rectangular, becoming bowed distally and angled and divided beneath distal phalanges (except terminal scansor). Scansors (terminal scansors of digit I not included in counts): 5-8-10-11-10 manus; 6-8-12-12-10 pes. Relative length of digits: $\mathrm{IV}>\mathrm{III}>\mathrm{I}>\mathrm{V}>\mathrm{I}$ (manus): $\mathrm{IV}>\mathrm{III} \sim \mathrm{V}>\mathrm{II}>\mathrm{I}$ (pes); interdigital webbing moderately developed between all digits of manus and digits I-IV of pes, absent between digits IV and V of pes.

Regenerated tail approximately equal to body length (TailL/SVL ratio 0.94), moderately thick, very slightly constricted at base, tapering gradually along distal $1 / 3$. No caudal tubercles; dorsal caudal scales squarish to oval, juxtaposed to subimbricate, eight rows per tail segment; subcaudal scales rectangular, approximately 1.5 times larger than dorsals, more strongly imbricating.

Osteology: Parietal bones paired; stapes imperforate. Phalangeal formula 2-3-4-5-3 for manus and 2-3-4-5-4 for pes. Presacral vertebrae 26 , including 3 anterior cervical (without ribs), 1 lumbar, and 2 sacral vertebrae; 5 pygal and 6.5 post pygal caudal vertebrae proximal to regenerated portion of tail (19.5 post pygal vertebrae to point of regeneration in specimen with relatively longest original tail, CAS 231838). Holotype and male paratypes with one pair of crescentic cloacal bones present at level of second to third pygal vertebrae. Endolymphatic sacs not enlarged extracranially. Epiphyses of long bones incompletely fused in juvenile specimen CAS 231838.

Coloration (in preservative): Dorsal ground color medium brown, with small (a single granule in extent) dark brown and cream marks forming vaguely pair of longitudinal stripes. Cream marks coalescing to form faint lines above forelimb insertion and over sacrum and pygal portion of tail. Cream lines on sacrum and tail base bordered laterally by dark brown lines. Pattern carries onto tail as an irregular buff to beige marking with dark brown borders. Regenerated portion of tail medium brown with irregularly scattered dark brown scales. Area from forelimb insertion to angle of jaws mottled with cream to beige spots. Dorsal surface of head darker than lateral. Labials dark brown with cream pigmentless spots. Iris coppery with brownish reticulations. Upper sur-


Figure 10. Holotype of Dierogekko thomaswhitei (MNHN 2004.0018) from vicinity of Gomen Mine, Mt. Taom, Massif d'Ouazangou-Taom, Province Nord, New Caledonia. Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.


Figure 11. Life photograph of male paratype of Dierogekko thomaswhitei (CAS 231877) illustrating the relatively bold patterning typical of some specimens. Photo by A.H. Whitaker.


Figure 12. Life photograph of female paratype of Dierogekko thomaswhitei (AMS R 161180) with the pale vertebral stripe barely distinguishable. Photo by A.H. Whitaker. faces of limbs similar to dorsum; palms, soles and subdigital surfaces brown to grayish-brown. Venter beige with brown punctations on most scales, pigmentation heaviest under limbs, at margins of flanks, and on heavily mottled chin and throat. Venter of both original and regenerated portions of tail light brown with scattered beige and dark brown scales.

In life the groin and throat of the holotype were yellow mottled with brown.
Variation.- Comparative mensural data for the holotype and paratypes are given in Table 5.

Meristic characters of paratypes are mostly similar to those of the holotype, and are mentioned hereafter if they differ. Mostly original tail of CAS 231838 is $102 \%$ of SVL. Precloacal pores in male paratypes in two series, anterior row with 12 (CAS 231837, 231877) or 14 (AMS R 161153, 161178,166975 ) pores, posterior row with 1 (AMS R 161178) pore, 2 pores (one on each side separated by 4 poreless scales; CAS 231877), 4 pores (two on left separated from two on right by four poreless scales; AMS R 161153, CAS 231837), or 5 pores (two on left separated from three on right by three poreless scales; AMS R 166975).

Middorsal stripe weakly developed, except on sacrum, in all paratypes, but distinctly lighter than remainder of dorsum in CAS 231838, AMS R 161153 and AMS R 166975. Dorsum nearly uniform yellowish-brown in CAS 231837. Loreal markings especially prominent and a dark streak from rostral to level of anterior border of orbit in CAS 231838. Venter pale in CAS 231837, almost lacking dark pigment all together in AMS R 161153. Regenerated portion of tail darker than original in all paratypes. In life AMS R 166975 had a pale yellow groin, while CAS 231837 and 231838 had pale, cream colored venters.

Distribution and Natural History.- This species is known only from Mount Taom, an ultramafic peak ( 1092 m maximum elevation), part of the large Massif d'Ouazangou-Taom in the northwestern Grande Terre of New Caledonia (Fig. 3). The vegetation of the summit area was briefly described by Whitaker et al. (2004). The types were collected in closed forest (AMS R 161153, CAS 231876) or at the border of closed forest and maquis (MNHN 2003.0016, CAS 231837-38, 231877, AMS R 166975, 161178, 161180) above the Gomen Mine ( 800 m ). Additional specimens were observed, but not collected, at lower elevations ( 350 m and 650 m) in maquis shrub (Fig. 13).

Other reptiles collected in the vicinity of the Gomen Mine on Mount Taom include Bavayia aff. exsuccida, Bavayia aff. montana, Eurydactylodes agricolae, Caledoniscincus


Figure 13. Habitat of Dierogekko thomaswhitei in maquis shrubland on Mt. Taom in the Massif d'OuazangouTaom. Province Nord. New Caledonia. Photo by A.H. Whitaker. aquilonius, C. austrocaledonicus, Marmorosphax aff. tricolor, Tropidoscincus boreus, a new species of skink allied to "Lygosoma" eurrotis (Sadlier et al. 2006), and a new genus and species of skink (Sadlier et al., in prep.). Hemidactylus frenatus and Caledoniscicncus haplorhinus have been found at lower elevations on the mountain (Whitaker et al. 2004).

Conservation Status.- Under favorable weather conditions, D. thomaswhitei were abundant on shrubby vegetation above the Gomen Mine and were present at mid-elevations as well. The area harbors the introduced Rattus rattus, and deer. feral cats, and pigs are numerous at lower elevations. The mine was inactive at the time of our visits to the site, but it has since been reopened by the Société Minière du Sud Pacifique (SMSP) and posses a potential threat to the habitat of this species. Although this gecko may also occur on adjacent peaks within the massif, we regard it as Critically Endangered.

## Dierogekko nehoueensis, Bauer, Jackman, Sadlier, and Whitaker, sp. nov.

 .Figures 14-16.Type Material. - Holotype: MNHN 2004.0019: Adult male: New Caledonia, Province Nord, Rivière Néhoué, $20^{\circ} 25^{\prime} 03^{\prime \prime} \mathrm{S}, ~ 164^{\circ} 13^{\prime} 15^{\prime \prime} \mathrm{E}$ (elevation 5 m ), collected by A.M. Bauer, R.A. Sadlier, T.

Jackman, S.A. Smith and G. Watkins-Colwell, 22 January 2003. Paratypes: CAS 231835: Adult female, CAS 231836: Adult male; same collection data as holotype. AMS R 166976: Adult female; same locality and collectors holotype, 25 January 2003. CAS 231855: Subadult female; New Caledonia, Province Nord, Rivière Néhoué, 20 km NW Koumac, $20^{\circ} 24^{\prime} 27.0^{\prime \prime} \mathrm{S}, 164^{\circ} 12^{\prime} 09.3^{\prime \prime} \mathrm{E}$ (elevation 5 m ), collected by A.H. Whitaker and V.A. Whitaker, 3 October 2001. CAS 231863: Adult male, CAS 231864, AMS R 161242-44: Adult females; New Caledonia, Province Nord, Dôme de Tiébaghi, 14 km NW Koumac, $20^{\circ} 27^{\prime} 37.8^{\prime \prime} \mathrm{S}, 164^{\circ} 11^{\prime} 11.2^{\prime \prime} \mathrm{E}$ (elevation 340 m ), collected by A.H. Whitaker and V.A. Whitaker, 17 October 2001.

Additional Material. - AMS R 166970, CAS 231854: New Caledonia, Province Nord, Rivière Néhoué, 20 km NW Koumac, $20^{\circ} 25^{\prime} 12.3^{\prime \prime} \mathrm{S}, 164^{\circ} 13^{\prime} 04.5^{\prime \prime} \mathrm{E}$ (elevation 5 m ), collected by A.H. Whitaker and V.A. Whitaker, 29 September 2001. AMS R 161246: same collection data as for CAS 231863.

Etymology. - The specific epithet is derived from the Rivière Néhoué, the type locality of the species and one of only three known localities where it occurs. The gallery forest along this small river is the type locality for two other species, Kanakysaurus viviparus and Eurydactylodes agricolae, and is one of the most herpetologically important lowland sites in the Province Nord. It has previously been recognized as having high conservation value (Veillon et al. 1999).

Diagnosis. - Dierogekko nehoueensis can be distinguished from all congeners on the basis of the following combination of characters: size relatively small (to 40.3 mm SVL ), $1-2$ internasal scales; distal subdigital lamellae divided; male preanal pores in two rows ( 12 in anterior row, 5-8 in posterior row). Narrow beige and dark brown lines bordering dorsal pale region well developed, dark brown line medial to beige stripe present from lumbar region onto tail base.

Description (based on holotype).- Adult male. SVL 40.3 mm ; TailL 36.2 mm (distal 32.1 mm regenerated). Head moderately long (HeadL/SVL ratio 0.31 ), relatively wide (HeadW/HeadL ratio 0.70 ), depressed (HeadH/HeadL ratio 0.34 ), weakly set off from relatively thick neck. Loreal region without inflated canthal area; interorbital region slightly depressed. Snout short (SnEye/HeadL ratio 0.33), blunt; longer than eye diameter (OrbD/SnEye ratio 0.64); scales on snout and forehead small, rounded, granular to weakly conical, homogeneous; scales on snout much larger than those on occipital region. Eye moderately large (OrbD/HeadL ratio 0.21 ); pupil vertical with crenelated margins; supraciliaries short, bearing two elongate spines near posterodorsal margin of orbit. Ear opening oval, angled posterodorsally at an angle of $45^{\circ}$ from horizontal, relatively small (EarL/HeadL ratio 0.10 ); eye to ear distance greater than diameter of eyes (EyeEar/OrbD ratio 1.20). Rostral much wider ( 2.0 mm ) than deep ( 0.9 mm ), nearly completely divided by rostral crease, except near margin of lip. Two relatively small supranasals separated by one very large pentagonal internasal. Rostral in contact with first supralabials, nostrils, supranasals and internasal. Nostrils rounded, each surrounded by supranasal, rostral, first supralabial, nasal and two postnasals; nasal narrowly separating two granues from nostril rim; supralabial in very narrow contact with nostril. At least four rows of small scales separate orbit from supralabials. Mental triangular, wider $(1.2 \mathrm{~mm})$ than deep ( 1.0 mm ). A single enlarged ( $\sim 12$ times size of granular throat scales) irregular, hexagonal postmental, anterior apex narrowest, bordered by mental, first infralabials, and four enlarged chin shields, two posteriorly and one each posterolaterally. Two to three scale rows posterior to postmental and medial to infralabials enalrged relative to remainder of chin and throat scales. Supralabials to midorbital position $7 / 8$; total enlarged supralabials $9 / 10$ supralabial scales to angle of jaws 13/14. Enlarged infralabials $9 / 9$; infralabials to angle of jaws $12 / 12$. Interorbital scale rows across narrowest point of frontal bone 15 .

Body slender, elongate (TrunkL/SVL ratio 0.43); no ventrolateral folds. Dorsal scales smooth, granular, homogeneous. Ventral scales larger than dorsals, smooth, with rounded free margins, subimbricate to imbricate, roughly uniform in size across most of venter, slightly enlarged in precloacal region. Approximately 142 scale rows around midbody. Gular region with homogeneous, smooth granular scales, equivalent in size to dorsal granules.

No enlarged precloacal or femoral scales; precloacal pores relatively small, in two angled series in adjacent scale rows; anterior continuous series of 12 pores, posterior continuous series of 6 pores. Two enlarged, smooth, conical, somewhat laterally projecting cloacal spurs, anterodorsal spur larger.

Scales on palm and sole smooth, rounded. Scalation on dorsal surfaces of limbs similar to body dorsum. Fore and hindlimbs short and thick (ForeaL/SVL ratio 0.13; CrusL/SVL ratio 0.15 ). Digits moderately dilated; claws well developed and recurved on digits $\mathrm{II}-\mathrm{V}$; claw much reduced and less strongly recurved on digit I, situated between asymmetrical distal pads (lateral pad approximately twice size of medial). Basal subdigital lamellae broad, rectangular, becoming bowed distally and angled and divided beneath distal phalanges (except terminal scansor). Scansors (terminal scansors of digit I not included in counts): 5-9-11-12-9 manus; 5-10-13-12-11 pes. Relative length of digits: $\mathrm{IV}>\mathrm{III}>\mathrm{II}>\mathrm{V}>\mathrm{I}$ (manus); $\mathrm{IV}>\mathrm{III} \sim \mathrm{V}>\mathrm{I}>\mathrm{I}$ (pes); interdigital webbing moderately developed between all digits of manus and digits I-IV of pes, absent between digits IV and $V$ of pes. Regenerated tail approximately equal to body length (TailL/SVL ratio 0.99), thick, slightly constricted at base, tapering gradually along distal $1 / 3$. No caudal tubercles; dorsal caudal scales squarish with rounded free margins,juxtaposed to submibricate; subcaudal scales slightly larger than dorsals, more strongly imbricating.

Osteology: Parietal bones paired; stapes imperforate. Phalangeal formula 2-3-4-5-3 for manus and 2-3-4-5-4 for pes. Presacral vertebrae 26 , including 3 anterior cervical (without ribs), 1 lumbar, and 2 sacral vertebrae; 5 pygal and 0.5 post pygal caudal vertebrae proximal to regenerated portion of tail (approximately 26 post pygal vertebrae in original tail of CAS 231836 and at least 23 in CAS 231835 - divisions in small, irregular terminal vertebrae difficult to discern). Male paratypes with one pair of crescentic cloacal bones present, flared posterolaterally, at level of second to third pygal vertebrae (cloacal bones lacking in female holotype). Endolymphatic sacs not enlarged extracranially.

Coloration (in preservative): Flanks mid-brown fading to gray-brown on lower margins. A broad middorsal, yellowish-brown stripe extending from snout to tail base, bordered laterally by two narrow stripes, a more medial cream stripe (approximately 3 granular scales in width) running
from posterodorsal margin of orbit to tail base, becoming thicker (approximately 5 granular scales in width) on head and nape and lumbar and sacral regions, and a narrower ( 2 granular scales in width) dark brown lateral stripe, more-or-less continuous, but interrupted in several places along the trunk. From lumbar region to tail base an additional thin ( $2-3$ granular scales in width) dark brown stripe borders the cream stripe medially. Scattered dark pigment spots in wide middorsal stripe, especially posteriorly. A thick dark stripe from nostril to anterior and ventral margins of orbit, separated from supralabials by a narrow light brown border and bounded above by pale beige patch extending from supranasals to anterior of orbit and bisected by anterior extention of the yellowishbrown middorsal stripe. Area between ear and angle of jaw pale grayish-beige. Labials mottled brown with cream (pigmentless) spots near sutures. Iris opalescent with brownish reticulations. Limbs mid-brown with darker and ligher mottling; palms, soles and subdigital surfaces brown to grayish-brown. Dorsum of regenerated tail light brown with numerous irregular dark markings, especially posteriorly. Tail venter as dorsum, but wirth fewer dark markings. Venter buff with light scattering of brown pigment.

In life venter a mottled yellow.
Variation.- Comparative mensural data for the holotype and paratypes are given in Table 6. Meristic characters of paratypes are mostly similar to those of the holotype, and are mentioned hereafter if they differ. Original tails of CAS 231835 and $231836114 \%$ and $106 \%$ of SVL, respectively. Two internasal scales in AMS R 161242, all other paratypes and non-types as holotype. Precloacal pores in male paratypes in two series, anterior row with 12 pored scales in continuous row (CAS 231836) or with a single poreless scale separating left and right series of 6 pored scales (CAS 231863). Posterior series with continuous row of 5 (CAS 231836) or 8 (CAS 231863) pores.

Dorsal patterning strongly demarcated, similar to holotype in AMS R 166976 (Fig. 15) and CAS 231836 and in juvenile non-types AMS R 166970 and CAS 231854-55. Original tail in CAS 231836 with narrow middorsal mid- to dark brown stripe paralleled by thicker cream stripes. These in turn bounded laterally by variably well developed narrow dark brown borders. Middorsal stripe lighter than flanks, but without striped cream or dark brown borders and original tail with series of contiguous gray-brown blotches on a dark brown background in CAS 231835. Dorsum nearly uniform with varying degrees of development of light brown punctations forming incomplete longitudinal dorsolateral lines (AMS R 161242-43) or with dark-bordered light spots forming distinct rows of ocelli (AMS R 161244, CAS 231864), sometimes contrastings strongly with the dorsal background (AMS R 161246, CAS 231863) (Fig. 16).

Distribution and Natural History.- This species is known from three localities on or in relatively close proximity to the ultramafic Dôme de Tiébaghi ( 599 m maximum elevation), both just north of Koumac in the far northwest of the Province Nord of New Caledonia (Fig. 3). These include a lowland site at the Rivière Néhoué, a mid-elevation ( 340 m ) site on the western slopes of the massif near Paagoumène, and from two adjacent sites in the headwaters of the Fridoline catchment. The Rivière Néhoué locality comprises a flood-prone, lowland gallery (vallicole) forest on deep alluvial soil adjacent to the river at $<10 \mathrm{~m}$ elevation (Fig. 17). The habitat is typified by a relatively complete canopy, sparse understory vegetation, deep leaf litter, and numerous logs and debris on the forest floor. Previous descriptions of this site have been published by Henkel and Böhme (2001) and Schröder and Röll (2002). The vegetation of Tiébaghi has been discussed and illustrated by Holloway (1979). Maquis vegetation occurs on the lower slopes and a low dense forest association that is restricted to Tiébaghi occurs at higher elevations (Holloway 1979). The specimens from the upper valleys on the slopes of the Dôme de Tiébaghi were collected in dense closed forest, under stones by day and active foraging on subcanopy shrubs at night. Specimens form the Fridoline catchment (Fig. 18) were in tall maquis shrubland with Gymnostoma and at lower eleva-
tions ( $60-80 \mathrm{~m}$ ) they were present in a narrow band of riparian forest along a stream bank. At mid-elevation they were found in low maquis. Most of those from Rivière Néhoué were collected under logs on soil, but one (AMS R 166969) was active at night on a shrub. Two adult female specimens (CAS 231835, AMS R 166976) collected in late January are gravid and contain two eggs each.

At Néhoué, D. nehoueensis cooccurs with a diverse herpetofaunal assemblage including Bavayia aff. exsuccida, B. aff. cyclura, Eurydactylodes agricolae, Rhacodactylus chahoua, Lepidodactylus lugubris, Hemidactylus frenatus, Caledoniscincus aff. austrocaledonicus, C. aquilonius, C. festivus, Lioscincus nigrofasciolatus, the newly described Kanakysaurus viviparus, and the introduced frog Litorea aurea. At Tiébaghi it is found with several of these species as well as Rhacodactylus auriculatus and Caledoniscincus haplorhinus (Whitaker et al. 2004).

Conservation Status.- Dierogekko nehoueensis appears to be relatively common at all localities where it has been found. Although the difference in habitat suggests that it may be fairly catholic in its requirements and may occur in other patches of suitable habitat in the region, subsequent searches at a range of localities at low- to mid-elevation around the Dôme de Tiébaghi have so far failed to locate further populations. The known localities are impacted by a variety of threats. Potential introduced predators, including rats and cats, are present at all sites and the Rivière Néhoué is also affected by pigs, cattle and deer (Whitaker Consultants Limited 2002; Whitaker et al. 2004). The Rivière Néhoué site is one of few remaining gallery forest patches in the lowlands of northwestern New Caledonia. The locality is currently administered as a recreational reserve, but the area is small and it experiences intensive human use. Further. Néhoué has been invaded


Figure 17. Habitat of Dierogekko nehoueensis in lowland gallery forest at the type locality of Rivière Néhoué, Province Nord, New Caledonia. Most specimens from this site were collected under logs on the ground. Photo A.H. Whitaker.


Figure 18. Habitat of Dierogekko nehoueensis in low maquis at Fridoline, Tiébaghi massif, Province Nord, New Caledonia. Photo A.H. Whitaker. by the introduced ant Wasmannia auropunctata (Sadlier et al. 2004), which is known to greatly reduce gecko abundance and has been associated with local extirpations of some lizard species (Jourdan et al. 2000, 2001). The isolated closed forest remnant on the western slopes of Dôme de Tiébaghi may be at risk from activities associated with nickel mining on the peak. Although the
locality where D. nehoueensis was collected is not protected, two similar forested areas on the perimeter of the plateau have been set aside as botanical reserves. The species is here regarded as Endangered.

Remarks. - The existence of this species was first noted by Henkel and Böhme (2001) who recorded the presence of Bavayia validiclavis at the type locality of Eurydactylodes agricolae ("circa 20 km north of Koumac, NW New Caledonia"), apparently at the Rivière Néhoué locality where our material was subsequently collected. A specimen of $D$. nehoueensis was also illustrated (as B. validiclavis, from "north of Koumac") by Seipp and Henkel (2000a, 2000b), and Schröder and Röll (2002) also referred to D. nehoueensis from Néhoué as B. validiclavis.

## Dierogekko insularis Bauer, Jackman, Sadlier, and Whitaker, sp. nov.

Figures 19-22.
Type Material.- Holotype: MNHN 2004.0020 (formerly AMS R 161069): Adult male; New Caledonia, Province Nord, Îles Belep, Île Art, Wênè Côgat, northern plateau, 2 km E Waala, $19^{\circ} 42^{\prime} 52.7^{\prime \prime} \mathrm{S}$, $163^{\circ} 39^{\prime} 37.6^{\prime \prime} \mathrm{E}$ (elevation 240 m ), collected by A.H. Whitaker and V.A. Whitaker 23 May 2002. Paratypes: AMS R 166971-72, CAS 231858: Adult male, CAS 231859: Adult female; New Caledonia, Province Nord, Île Yandé, Mariri [stream], 32 km NW Poum, $20^{\circ} 02^{\prime} 39.4^{\prime \prime} \mathrm{S}, 163^{\circ} 47^{\prime} 43.4^{\prime \prime} \mathrm{E}$ (elevation 20 m ), collected by A.H. Whitaker and V.A. Whitaker, 7 October 2001. AMS R 161067, CAS 231865: Adult males; New Caledonia, Province Nord, Îles Belep, Île Pott, Pânan, $19^{\circ} 35^{\prime} 06.5^{\prime \prime} \mathrm{S}$, $163^{\circ} 35^{\prime} 06.9^{\prime \prime} \mathrm{E}$ (elevation 80 m ), collected by A.H. Whitaker and V.A. Whitaker, 27 May 2002. AMS R 161075, CAS 231867-68: Adult males; same data as holotype.

Additional Material.- AMS R166973-74, CAS 231856-57: same data as AMS R 166971. CAS 231866: same data as CAS 231865. AMS R 161070-71, CAS 231869: same data as holotype.

Etymology.- The specific epithet insularis refers to the fact that this species is known only from islands in the far north of New Caledonia. These include Île Art and Île Pott in the Îles Belep, the northernmost ultramafic outliers of New Caledonia, and Île Yandé, NNW of Poum.

Diagnosis.- Dierogekko insularis can be distinguished from all congeners on the basis of the following combination of characters: size intermediate (to 41.4 mm SVL), $1-2$ internasal scales; distal subdigital lamellae divided; male preanal pores in one or two rows (anterior row 9-12, posterior row, when present, 1-8). Midvertebral region darker than remainder of dorsum, dark longitudinal borders of dorsal pale region well developed, beige stripes reduced to a series of spots.

Description (based on holotype).- Adult male. SVL 41.4 mm ; TailL 49.6 mm (distal 19.8 mm regenerated). Head relatively short (HeadL/SVL ratio 0.27), relatively wide (HeadW/HeadL ratio 0.70 ), somewhat depressed (HeadH/HeadL ratio 0.40 ), weakly set off from relatively thick neck. Loreal region without inflated canthal area; interorbital region slightly depressed. Snout relatively long (SnEye/HeadL ratio 0.42), blunt; longer than eye diameter (OrbD/SnEye ratio 0.63); scales on snout and forehead small, rounded, granular to weakly conical, homogeneous; scales on snout larger than those on occipital region. Eye large (OrbD/HeadL ratio 0.27); pupil vertical with crenelated margins; supraciliaries short, bearing 3 elongate spines near posterodorsal margin of orbit. Ear opening oval, angled posterodorsally at an angle of $45^{\circ}$ from horizontal, relatively large (EarL/HeadL ratio 0.14); eye to ear distance approximately same as diameter of eyes (EyeEar/OrbD ratio 0.99 ). Rostral much wider ( 2.1 mm ) than deep ( 1.1 mm ), incompletely divided dorsally. Two moderately enlarged supranasals separated by two pentagonal internasals. Rostral in contact with first supralabials, nostrils, supranasals and internasals. Nostrils rounded, each surrounded by supranasal, rostral, first supralabial, nasal and two postnasals. At least four rows of small scales separate orbit from supralabials. Mental triangular, wider ( 1.2 mm ) than deep ( 1.0 mm ). Two enlarged ( $\sim 16$ times size of granular throat scales) irregular, polygonal postmentals separated by first infral-
abials from mental, bordered by first infralabials and posteriorly and posterolaterally by four enlarged chin shields each. Two to three scale rows posterior to postmental and medial to infralabials enlarged relative to remainder of chin and throat scales. Supralabials to midorbital position 9/8; total enlarged supralabials $11 / 10$; supralabial scales to angle of jaws $15 / 13$. Enlarged infralabials 10/10; infralabials to angle of jaws $12 / 14$. Interorbital scale rows across narrowest point of frontal bone 17 .

Body slender, moderately elongate (TrunkL/SVL ratio 0.40); no ventrolateral folds. Dorsal scales smooth, granular, homogeneous. Ventral scales larger than dorsals, smooth, oval anteriorly to circular posteriorly, all with rounded free margins, subimbricate to imbricate, roughly uniform in size across venter. Approximately 137 scale rows around midbody. Gular region with homogeneous, smooth granular scales, equivalent in size to dorsal granules.

No enlarged precloacal or femoral scales; precloacal pores relatively small, in two adjacent angled series, anterior continuous row of 12 pores, posterior continuous row of four pores; no femoral pores. One enlarged, smooth, somewhat laterally projecting cloacal spur.

Scales on palm and sole smooth, rounded. Scalation on dorsal surfaces of limbs similar to body dorsum. Fore and hindlimbs short and thick (ForeaL/SVL ratio 0.13; CrusL/SVL ratio 0.14 ). Digits moderately dilated; claws well developed and recurved on digits II-V; claw much reduced and less strongly recurved on digit I, situated between asymmetrical distal pads (lateral pad approximately twice size of medial). Basal subdigital lamellae broad, rectangular, becoming bowed distally and angled and divided beneath distal phalanges (except terminal scansor). Scansors (terminal scansors of digit I not included in counts): 4-8-9-10-9 manus; 5-8-10-11-9 pes. Relative length of digits: $\mathrm{IV}>\mathrm{III}>\mathrm{I}>\mathrm{V}>\mathrm{I}$ (manus); $\mathrm{IV}>\mathrm{III} \sim \mathrm{V}>\mathrm{I}>\mathrm{I}$ (pes): interdigital webbing moderately developed between digits I-IV of pes, weakly developed between all digits of manus and absent


Figure 19. Holotype of Dierogekko insularis (MNHN 2004.0020) from Wênè Côgat, Île Art, Îles Belep, Province Nord, New Caledonia. Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.


Figure 20. Life photograph of Dierogekko insularis from Pânan, Île Pott, Îles Belep, Province Nord, New Caledonia, with very well-developed margins to the dorsal stripe and numerous darkly pigmented markings. Photo by A.H. Whitaker.


Figure 21. Life photograph of male paratype of Dierogekko insularis (CAS 231867) from Wênè Côgat, Île Art. Îles Belep. Province Nord. New Caledonia, with a distinctly pale vertebral stripe with a moderately well-developed border and no vertebral markings. Photo by A.H. Whitaker.


Figure 22. Life photograph of male paratype of Dierogekko insularis (AMS R 161075) from Wênè Côgat, Île Art. Îles Belep, Province Nord. New Caledonia, with a poorly differentiated vertebral stripe bordered by a series of pale spots rather than a continuous line. Photo by A.H. Whitaker.
between digits IV and V of pes. Partly regenerated tail longer than body length (TailL/SVL ratio 1.20), thick, slightly constricted at base, tapering gradually along distal half. No caudal tubercles; dorsal caudal scales squarish to oval, juxtaposed to subimbricate, eight rows per tail segment; subcaudal scales approximately 1.5 times larger than dorsals, rectangular with rounded free edges, more strongly imbricating.

Osteology: Parietal bones paired; stapes imperforate. Phalangeal formula 2-3-4-5-3 for manus and 2-3-4-5-4 for pes. Presacral vertebrae 26, including 3 anterior cervical (without ribs), 1 lumbar, and 2 sacral vertebrae; 5 pygal and 12.5 post pygal caudal vertebrae proximal to regenerated portion of tail of holotype. Holotype and all other male specimens with one pair of crescentic cloacal bones present at level of second to third pygal vertebrae. Endolymphatic sacs not enlarged extracranially.

Coloration (in preservative): Dorsum medium brown with middorsal region slightly darker, demarcated by a pair of parasagittal series of faint beige spots ( $1-4$ granular scales in width) with dark brown posterolateral borders. Series of marks most strongly developed on sacrum. Area from snout through eye to above ear slightly darker than remainder of head. Labials mid-brown with scattered small cream spots. Iris golden brown with black reticulations. Flanks and lateral borders of throat dappled with cream to beige spots. Limbs similar to dorsum but with lighter and darker brown mottling; palms, soles and subdigital surfaces brown to grayish-brown. Tail dorsum with very faint pattern of parasagittal light brown stripes with irregular borders; scattered dark brown scales irregularly distributed. Venter beige with scattered brown punctations on individual scales, pigmentation heaviest under limbs and on lateral margins of chin. Tail venter more-or-less uniform light brown with a few scattered mid-brown scales.

In life no dorsal markings were evident on AMS R 166972 or CAS 231858.
Variation.- Comparative mensural data for the holotype and paratypes are given in Table 7. Meristic characters of paratypes are mostly similar to those of the holotype, and are mentioned hereafter if they differ. One internasal scale in AMS R 166971, 166972, CAS 231858-59, and 231868. All paratypes with only a single postmental, $\sim 8-20$ times size of chin granules, variable in shape, contacting posterior apex of mental. Precloacal pores in male paratypes in two series (Îles Belep) or a single series (Île Yandé). Île Yandé male paratypes with 12 precloacal pores in a continuous series (CAS 231858) or separated by a single poreless central scale into series of 7 (left) and 5 (right) pores (AMS R 166972); Île Pott paratypes with pores arranged in adjacent continuous series of 10 and 1 (CAS 231865) or 12 and 8 (AMS R 161067); Ille Art paratypes with pores arranged in adjacent continuous series of 12 and 1 (CAS 231867), 11 and 5 (CAS 231868), or 9 and 2 (AMS R 161075). Another Yandé male (non-type), CAS 231857, has two rows of precloacal pores, 13 and 5 , demonstrating that a second row of pores occurs in some males on all three of the islands.

Dorsal pattern as in holotype, but with crown of head and middorsal stripe yellowish brown in AMS R 161067, AMS R 161075 (Fig. 21), CAS 231857 and CAS 231865. Others specimens paler overall with middorsal stripe and especially crown of head more yellowish, remainder of dorsum grayish-brown; longitudinal markings with faint cream borders on sides of head, lateral margins of middorsal stripe demarcated by beige spots without, or with weakly developed, dark brown borders. Dorsal pattern bold, with continuous medial cream stripes ( $1-4$ granular scales in width) and lateral dark brown stripes ( $2-3$ granular scales in width) bordering yellowish brown middorsal stripe in remaining specimens (Fig. 19). AMS R 161070 and CAS 231867 (Fig. 20) very dark overall, with light markings light brown rather than cream. Most specimens with a dark line from snout through eye to nape, especially well developed in CAS 231859, in which it constrasts strongly with the paler middorsal stripe and crown. Same paratype with a sagittal dark line extending from rostral to middorsum of snout. Left side of middorsal and parasagittal markings interupted around left shoulder
in AMS R 166971. Juvenile non-types variable in pattern: weakly developed in CAS 231856 (20.2 mm SVL), bold in AMS R 166973 ( 18.2 mm SVL). Original portions of tails in most specimens with a broad central cream line with dark brown lateral borders. Venter, especially chin, more heavily pigmented in AMS R 161070, CAS 231857, 231867 and 231869 than in holotype.

Distribution and Natural History.-
This species is known from the Îles Belep and Île Yandé (Fig. 3). Until recently both groups had been unexplored herpetologically. Jouan $(1863,1864)$ briefly discussed reptiles on the Îles Belep. A new genus and species of skink, Kanakysaurus viviparus (Sadlier et al. 2004) has recently been identified from the Belep islands and two sites on the New Caledonian mainland. In the Belep islands, D. insularis has been found on both Île Art (Aar) and Île Pott (Phwoc). The southernmost point of Île Art is approximately 45 km north of the northern tip of the Grande Terre, and Île Pott lies about 3 km north of Île Art, approximately 65 km from the Grande Terre. The specimens from Île Pott and Île Yandé were collected in maquis vegetation (Fig. 23) while those on Ille Art were found in low, closed forest (Fig. 24). On Yandé, they were active at night on low bushes, exhibiting the characteristic nimbleness and agility of members of this genus (Whitaker Consultants Limited 2002). Two individuals from the Belep islands were found on an exposed clay bank (Whitaker et al. 2004). Paratype AMS R 166971, collected in October, 2001. contains two eggs.

At the type locality of Wênè Côgat D. insularis is sympatric with Eurydactylodes agricolae, Rhacodactylus aff. chahoua, $R$. aff. ciliatus, Caledoniscincus atropunctatus, C. aff. austrocaledonicus, Kanakysaurus viviparus, and Lioscincus nigrofasciolatus. At the paratype locality on Île Pott it co-occurs with Bavayia aff. cyclura, Eurydactylodes agricolae, Hemidactylus garnotii, Caledoniscincus haplorhinus, Cryptoblepharus novocaledoniae, and Kanakysaurus viviparus, while on Yandé it is sympatric with the first two skinks. In addition, several geckos and Litoria aurea are present in coastal localities on Yandé and Phoboscincus garnieri has been seen on Île Art (Whitaker et al. 2004).

Conservation Status.- Dierogekko insularis is abundant in both closed forest and maquis habitats on the Îles Belep, occurring in groups of up to eight on single shrubs (Whitaker et al. 2004), but these the vegetation types are at risk from the relatively frequent wild fires (Sadlier et al. 2004). Introduced rats and feral catas are present on Yandé and in the Belep islands. Unlike at most mainland sites where predation is only suspected, cats on Yandé are documented to eat small lizards (Whitaker et al. 2004). Although absent from the maquis, fire ants (Wasmannia auropunctata) are established on Yandé in lowland secondary forest and are also present on Île Art and Île Pott, and they pose a potential threat to gecko populations. The species is here regarded as Endangered.

Dierogekko poumensis Bauer, Jackman, Sadlier, and Whitaker, n. sp.

(Figs. 25-27)
Type Material.- Holotype: MNHN 2004.0021: Adult male; New Caledonia, Province Nord, Sommet Poum, vicinity telecommunications tower, Poum, $20^{\circ} 14^{\prime} 19^{\prime \prime} \mathrm{S}, 164^{\circ} 01^{\prime} 56^{\prime \prime}$ E (elevation 200 m ), collected by A.M. Bauer, R.A. Sadlier, T. Jackman, S.A. Smith and G. Watkins-Colwell, 25 January 2003. Paratypes: AMS R 166977-78, CAS 231841, 231850, 231852: Adult males, AMS R 166979-80, CAS 231839, 231851: Adult females; same collection data as holotype.

Additional Material.- AMS R 166981-89, CAS 231840, 231842-49, 231853, MCZ R 184130-33, MNHN 2004.0022-2004.0024, USNM 563360-61, YPM 15177-79: same collection data as holotype. AMS R 161205-07, CAS 231860-61: New Caledonia, Province Nord, Sommet Poum, 3 km S Poum, $20^{\circ} 15^{\prime} 44.2^{\prime \prime} \mathrm{S}, 164^{\circ} 02^{\prime} 06.6^{\prime \prime} \mathrm{E}$ (elevation 400 m ), collected by A.H. Whitaker and V.A. Whitaker, 11 October 2001.

Etymology.- The specific epithet poumensis refers to the occurrence of this species on Sommet Poum, the northernmost of the northwest ultramafic peaks of the Grande Terre. It is roughly sympatric with $D$. inexpectatus.

Diagnosis.- Dierogekko poumensis can be distinguished from all congeners on the basis of the following combination of characters: size small (to 38.3 mm SVL ), 1 internasal scale; distal subdigital scansors typically undivided or incompletely divided; male preanal pores in a single row of $8-11$. Crown of head mottled with beige spots, middorsal pale area bisected by irregular pale to mid-brown streak; cream and dark brown borders of dorsal pale region well demarcated; cream lines become bright white on sacrum or pygal portion of tail; original and regenerated tails typically with irregular yellowish- to rusty orange background wash.

Description (based on holotype).— Adult male. SVL 34.3 mm ; TailL 35.3 mm (distal 28.1 mm regenerated). Head moderately short (HeadL/SVL ratio 0.30), relatively wide (HeadW/HeadL ratio 0.66 ), not depressed (HeadH/HeadL ratio 0.42 ), weakly set off from relatively thick neck. Loreal region without inflated canthal area; interorbital region slightly depressed. Snout short (SnEye/HeadL ratio 0.35), blunt; longer than eye diameter (OrbD/SnEye ratio 0.64); scales on snout and forehead small, rounded, granular to weakly conical, homogeneous; scales on snout larger than those on occipital region. Eye moderately large (OrbD/HeadL ratio 0.22); pupil vertical with crenelated margins; supraciliaries short, bearing 2 elongate spines near posterodorsal margin of orbit. Ear opening eliptical, angled posterodorsally at an angle of $45^{\circ}$ from horizontal, moderately large (EarL/HeadL ratio 0.12); eye to ear distance greater than diameter of eyes (EyeEar/OrbD ratio 1.18). Rostral much wider ( 1.8 mm ) than deep ( 0.8 mm ), incompletely divided dorsally. Two moderately enlarged squarish supranasals separated by one large septagonal internasal. Rostral in contact with first supralabials, nostrils, supranasals and internasal. Nostrils rounded, each surrounded by supranasal, rostral, first supralabial, nasal and two postnasals. At least four rows of small scales separate orbit from supralabials. Mental triangular, wider ( 1.2 mm ) than deep ( 1.0 mm ). A single enlarged (15-20 times size of granular throat scales) symmetrical, octagonal postmental bordered by mental, first infralabials, and five enlarged chin shields. Two to three scale rows posterior to postmental and medial to infralabials enlarged relative to remainder of chin and throat scales. Supralabials to midorbital position $7 / 7$ total enlarged supralabials $9 / 8$; supralabial scales to angle of jaws $13 / 14$. Enlarged infralabials $9 / 8$; infralabials to angle of jaws $12 / 11$. Interorbital scale rows across narrowest point of frontal bone 16 .

Body slender, elongate (TrunkL/SVL ratio 0.41); no ventrolateral folds. Dorsal scales smooth, granular, homogeneous. Ventral scales slightly larger than dorsals, smooth, oval anteriorly to circular posteriorly, with rounded free margins, subimbricate to imbricate, roughly uniform in size across venter. Approximately 128 scale rows around midbody. Gular region with homogeneous, smooth
granular scales, equivalent in size to dorsal granules.

No enlarged precloacal or femoral scales; precloacal pores relatively small, in single continuous angled series of 11 ; no femoral pores. One (right) or two (left) enlarged, smooth, conical, somewhat laterally projecting cloacal spurs.

Scales on palm and sole smooth, rounded. Scalation on dorsal surfaces of limbs similar to body dorsum. Fore and hindlimbs short and thick (ForeaL/SVL ratio 0.13; CrusL/SVL ratio 0.16 ). Digits moderately dilated; claws well developed and recurved on digits II-V; claw much reduced and less strongly recurved on digit I, situated between asymmetrical distal pads (lateral pad approximately twice size of medial). Basal subdigital lamellae broad, rectangular, becoming bowed distally and angled and undivided or incompletely divided beneath distal phalanges. Scansors (terminal scansors of digit I not included in counts): 4-7-10-10-9 manus; 4-9-11-11-9 pes. Relative length of digits: $\mathrm{IV}>\mathrm{III}>\mathrm{II}>\mathrm{V}>$ I (manus); $\mathrm{IV}>\mathrm{III} \sim \mathrm{V}>\mathrm{I}>\mathrm{I}$ (pes); interdigital webbing moderately developed between all digits of manus and digits I-IV of pes, absent between digits IV and V of pes. Mostly regenerated tail approximately


Figure 25. Holotype of Dierogekko poumensis (MNHN 2004.0021) from Sommet Poum, Province Nord, New Caledonia. Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.


Figure 26. Life photograph of Dierogekko poumensis from Sommet Poum, Province Nord, New Caledonia, with bold dorsal markings. As is typical for this species, the markings at the tail base are bright white and the tail has orangish markings. Photo by A.H. Whitaker. equal to body length (TailL/SVL ratio 1.03 ), thick, slightly constricted at base, tapering gradually along distal $1 / 3$. No caudal tubercles; dorsal caudal scales squarish to rectangular with rounded free margins, juxtaposed to submibricate, eight rows per tail segment; subcaudal scales rectangular, approximately 1.5 times larger than dorsals, more strongly imbricating.

Osteology: Parietal bones paired: stapes imperforate. Phalangeal formula 2-3-4-5-3 for manus and 2-3-4-5-4 for pes. Presacral vertebrae 26, including 3 anterior cervical (without ribs), 1 lumbar, and 2 sacral vertebrae; 5 pygal and 6.5 post pygal caudal vertebrae proximal to regenerated portion of tail of holotype ( 12.5 post-pygal vertebrae to point of regeneration in paratype with longest original tail. CAS 231851). Male paratypes with one pair of crescentic cloacal bones present, flared posterolaterally, at level of second to third pygal vertebrae. Endolymphatic sacs not enlarged extracranially.

Coloration (in preservative): Mid-brown with a slightly lighter middorsal stripe mottled with beige spots, especially on the crown of the head. Middorsal stripe paralleled by a pair of parasagittal pale stripes from supranasals to tail, beige on trunk, but white from posterior of orbit to level of occiput and on sacrum and tail base. Middorsal stripe bisected on trunk by an irregular pale to midbrown stripe. Beige to white parasagittal stripe bordered laterally by a more-or-less continuous dark brown border: a more incomplete dark brown border medially. Thick dark stripe from nostril through eye to above ear, continuous with lateral border of pale parasagittal stripe. Labials with alternating pattern of mid- to dark brown and cream. Flanks mottled grayish-brown. Limbs similar
to upper flanks and mottled with lighter and darker markings; palms, soles and subdigital surfaces brown to grayish-brown. Pale parasagittal stripes well defined on tail base, with dark borders; pattern fading rapidly distally along tail. Regenerated portion of tail mottled light to mid-brown. Venter beige with many scattered dark brown scales, pigmentation heaviest under limbs, around cloaca and on throat, which has a marbled appearance. Venter of both original and regenerated portions of tail an uneven grayish-brown.

Variation.- Comparative mensural data for the holotype and paratypes are given in Table 8. Body size ranged from 24.3 mm (AMS R 166982 , juvenile non-type) to 38.3 (female paratype CAS 231841). Mostly original tail of CAS 231850 is $107 \%$ of SVL. Meristic characters of paratypes are mostly similar to those of the holotype. Precloacal pores in male paratypes in a single continuous series of 8 (AMS R 166978), 10 (CAS 231850, 231852), or 11 (AMS R 166977).

Color pattern is relatively uniform among the large series of specimens examined. The pale lines on the sacrum are almost always bright white (Figs. 25-26). The pale middorsal stripe is somewhat less-well demarcated than in the holotype in AMS R 166988-89, AMS R 161205, CAS 231848, USNM 563361, and YPM 15178. MCZ R 184132 and AMS R 166989 have somewhat less heavily pigmented venters than the holotype. Tail of juvenile specimen AMS R 166982 distinctly orange-red in life. Whitaker Consultants Limited (2002) noted the orange tint of tails of this species (Fig. 25) and also suggested that the tail was thickened relative to other Dierogekko species.

Distribution and Natural History.- This species is known only from Sommet Poum ( 414 m maximum elevation) (Fig. 3). Its distribution over the massif appears patchy but it is known from several localities from the vicinity of the town of Poum in the north to Canne Stream on Sommet Sud in the south. All sites are in maquis shrubland (Fig. 28), from elevations of 10 m to the highest levels of the summit plateau. The large series was collected in a span of about two hours. All animals collected with the types were active on low (approximately 1 m ) maquis shrubs along the service track to the telecommunications tower on the north slope of Sommet Poum (Fig. 29). As many as five geckos were active on a single plant. Animals appeared to be actively foraging on the twigs and foliage when captured. When approached closely some geckos dropped to the base of bushes as has been reported for roosting chameleons (Parcher 1974). Many females contained two eggs including the largest specimens examined, paratype CAS 231841, as well as non-types AMS

R 166986-87, CAS 231844 and YPM 15179, collected in January 2003, and AMS R 161205-06 and CAS 231860, collected in October 2001.

Dierogekko poumensis is syntopic with Eurydactylodes agricolae and another new species of Dierogekko (see below) on the plateau of Sommet Poum, and with Oedodera marmorata and Hemidactylus frenatus at the low elevation sites. Other sympatric taxa include Cryptoblepharus novocaledonicus and an unidentified Caledoniscincus, as well as a large skink, possibly Phoboscincus garnieri, in maquis on top of the massif, and the common lowland species (Caledoniscincus atropunctatus, C. aff. austrocaledonicus, C. haplorhinus, Lioscincus nigrofasciolatus) occur near sealevel on the lower slopes of the mountain (Whitaker et al. 2004).

Conservation Status.-Dierogekko poumensis is extremely common at its type locality and occurs in lesser abundance at other sites on the massif. However, the total area of Sommet Poum is small and populations of $D$. poumensis are patchy. A nickel mine is currently being operated at the northern end of the massif and there are plans to extend the pit to the summit plateau. Wild fires are a relatively frequent occurrence and since 2001 a fire has destroyed a large area of maquis on the plateau where these geckos were formerly common. An added threat is that fire ants have recently established in closed forest remnants on the


Figure 28. Maquis shrubland on the plateau of Sommet Poum, Province Nord, New Caledonia. Photo by A.H. Whitaker.


Figure 29. Maquis shrubs at type locality of Dierogekko poumensis near the telecommunications tower at approximately 200 m elevation, Sommet Poum, Province Nord. New Caledonia overlooking Île Mouac (left) and Île Tuany (right) off the northwest coast of the Grande Terre. As many as five individuals were found in a single shrub. Photo by A.M. Bauer. plateau with a consequent decimation of gecko populations (Jourdan et al. 2000, 2001). Both introduced rats and feral cats occur on Sommet Poum, but as on most northwestern peaks, direct evidence of gecko predation is lacking (Whitaker et al. 2004). Given the highly restricted known range of this species and serious threats to its habitat. we regard it as Critically Endangered.

## Dierogekko inexpectatus Bauer, Jackman, Sadlier, and Whitaker, sp. nov.

Figures 30-31.
Type Material.- Holotype: MNHN 2004.0025 (formerly AMS R 161222): Adult female; New Caledonia, Province Nord, Sommet Poum, Paevala. 2 km S Poum, $20^{\circ} 15^{\prime} 05.6^{\prime \prime} \mathrm{S}, 164^{\circ} 01^{\prime} 22.4^{\prime \prime} \mathrm{E}$ (elevation 320 m ), collected by A.H. Whitaker and V.A. Whitaker 15 October 2001.

Etymology.- The species name inexpectatus means unexpected and refers to the occurrence of this second species of Dierogekko from the small, relatively low elevation Poum Massif. When originally discovered it was not recognized as being distinct from the smaller D. poumensis (Whitaker Consultants Limited 2002).

## Diagnosis.- Dierogekko inexpectatus

 can be distinguished from all congeners on the basis of the following combination of characters: size relatively small ( 39.5 mm in unique type), three internasal scales; distal subdigital lamellae divided; [male preanal pore condition unknown]. Cream stripes uniform on dorsum, becoming wider on tail base; small cream spots on area between forelimb insertion and loreals.Description (based on holotype).- Adult female. SVL 39.5 mm ; TailL 36.2 mm (distal 25.8 mm regenerated). Head relatively short (HeadL/SVL ratio 0.27), wide (HeadW/HeadL ratio 0.68), somewhat depressed (HeadH/ HeadL ratio 0.39 ), weakly set off from relatively thick neck. Loreal region without inflated canthal area; interorbital region slightly depressed. Snout moderately elongate (SnEye/HeadL ratio 0.44), blunt; much longer than eye diameter (OrbD/SnEye ratio 0.54); scales on snout and forehead small, rounded, granular to weakly conical, homogeneous; scales on snout much larger than those on occipital region. Eye relatively large (OrbD/HeadL ratio 0.24); pupil vertical with crenelated margins; supraciliaries short, bearing three elongate spines near posterodorsal margin of orbit. Ear opening elliptical, angled posterodorsally at an angle of $45^{\circ}$ from horizontal, large (EarL/HeadL ratio 0.14); eye to


Figure 30. Holotype of Dierogekko inexpectatus (MNHN 2004.0025) from Paevala, Sommet Poum, Province Nord, New Caledonia. Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.


Figure 31. Life photograph of holotype of Dierogekko inexpectatus (MNHN 2004.0025) from Paevala, Sommet Poum, Province Nord, New Caledonia. Photo by A.H. Whitaker. ear distance greater than diameter of eyes (EyeEar/OrbD ratio 1.20 ). Rostral wider ( 1.7 mm ) than deep ( 1.1 mm ), incompletely divided dorsally. Two moderately enlarged supranasals separated by three internasals, one anterior and two posterior. Rostral in contact with first supralabials, nostrils, supranasals and all three internasals. Nostrils rounded, each surrounded by supranasal, rostral, first supralabial, nasal and two postnasals. At least four rows of small scales separate orbit from supralabials. Mental triangular, wider (1.2 mm ) than deep ( 1.0 mm ). A single enlarged ( $15-20$ times size of granular throat scales) hexagonal postmental, anterior apex narrowest, bordered by mental, first infralabials, and four enlarged chin shields, two posteriorly and one each posterolaterally. Two to three scale rows posterior to postmental and medial to infralabials enlarged relative to remainder of chin and throat scales. Supralabials to midorbital position $8 / 7$; total enlarged supralabials $10 / 10$; supralabial scales to angle of jaws $14 / 14$. Enlarged infralabials $8 / 8$; infralabials to angle of jaws $11 / 13$. Interorbital scale rows across narrowest point of frontal bone 17 .

Body slender, elongate (TrunkL/SVL ratio 0.44) no ventrolateral folds. Dorsal scales smooth, granular, homogeneous. Ventral scales larger than dorsals, smooth, hexagonal and subimbricate to imbricate, roughly uniform in size across venter. Approximately 151 scale rows around midbody. Gular region with homogeneous, smooth granular scales, equivalent in size to dorsal granules. No
enlarged precloacal or femoral scales; no precloacal or femoral pores. No enlarged cloacal spurs.
Scales on palm and sole smooth, rounded. Scalation on dorsal surfaces of limbs similar to body dorsum. Fore and hindlimbs short and thick (ForeaL/SVL ratio 0.12; CrusL/SVL ratio 0.14). Digits moderately dilated; claws well developed and recurved on digits II-V; claw much reduced and less strongly recurved on digit I, situated between asymmetrical distal pads (lateral pad approximately twice size of medial). Basal subdigital lamellae broad, rectangular, becoming bowed distally and angled and divided beneath distal phalanges (except for terminal scansor). Scansors (terminal scansors of digit I not included in counts): 6-9-12-12-9 manus; 6-10-12-11-9 pes. Relative length of digits: $\mathrm{IV}>\mathrm{III}>\mathrm{I}>\mathrm{V}>\mathrm{I}$ (manus); $\mathrm{IV}>\mathrm{III} \sim \mathrm{V}>\mathrm{II}>\mathrm{I}$ (pes); interdigital webbing moderately well developed between all digits of manus and digits I-IV of pes. Regenerated tail shorter than SVL (TailL/SVL ratio 0.92 ), thick, slightly constricted at base, tapering sharply along distal $1 / 3$. No caudal tubercles; dorsal caudal scales rectangular, juxtaposed, eight rows per tail segment; subcaudal scales larger than dorsals.

Osteology; Parietal bones paired; stapes imperforate. Phalangeal formula 2-3-4-5-3 for manus and 2-3-4-5-4 for pes. Presacral vertebrae 26, including 3 anterior cervical (without ribs), 1 lumbar, and 2 sacral vertebrae; 5 pygal and 4.5 post pygal caudal vertebrae in original tail of holotype. Endolymphatic sacs not enlarged extracranially.

Coloration (in preservative): Dorsal ground color brown, with a pair of thin (2-3 granular scales in width), cream, parasagittal stripes extending from posterodorsal margin of orbit on to tail base; stripes relatively uniform on dorsum, becoming thicker and less well defined on original portion of tail. Stripes bordered by narrow (1-2 granular scales in width) dark brown margins, more well developed laterally than medially. Vertebral area lighter than than dorsum lateral to stripes. Area in front of forelimb insertion and below cream stripe as far anterior as loreal region darker brown than dorsum, with scattered, small, irregular cream colored spots. Labial scales mid- to dark brown with cream gaps bracketing sutures between scales. Iris blackish. Flanks light brown. Limbs mottled; palms, soles and subdigital surfaces brown to grayish-brown. Regenerated portion of tail midbrown with irregular darker markings, some longitudinally oriented. Venter beige with scattered small, dark punctations on individual scales; chin mottled. Tail venter light brown, with relatively uniform brown pigment flecks across all scales: scattered larger dark brown markings irregularly distributed. Venter of regenerated portion of tail becoming darker distally.

Distribution and Natural History. - This species is known from a single specimen collected beneath a stone in deep leaf litter in closed forest at Paevala ( 320 m ) on Sommet Poum, at the far northwest of the Grande Terre (Fig. 3). Dierogekko inexpectatus cooccurs with its congener D. poumensis. Other reptile species occurring on Sommet Poum are listed under the account of the latter species.

Conservation Statcs.- As only a single individual of this species was collected, despite the large number of $D$. poumensis found. it is possible that $D$. inexpectatus may be very limited in its distribution. Although it may occur nearby in unsampled areas it has not been found during searches of any other localities and a recent resurvey of the type locality failed to find further individuals. The threats facing lizard populations on Sommet Poum (mining, wild fires, fire ants, introduced mammalian predators) have been discussed under $D$. poumensis. We provisionally regard $D$. inexpectatus as Critically Endangered, but further data are required to assess the real threats to its survival.

## Comparisons among Species

As noted in the introduction. Dierogekko spp. are highly conservative in morphology, and differ little in most respects. All species can be unambiguously diagnosed on the basis of mtDNA data,
but no single morphological features have been identified that will serve to distinguish them. Even the few putatively diagnostic combinations of features must be considered as provisional in that they will only serve to distinguish the species based on the degree of variation known to exist in the specimens available. Sample sizes, however, are small for most species and larger samples might reveal more extensive overlap in features such as size and preanal pore counts. In practice, species of Dierogekko are most easily assigned to species on the basis of locality. Only on Sommet Poum do two species occur in sympatry ( $D$. poumensis, $D$. inexpectatus). The former species may be distinguished from the latter by its smaller size (maximum 38.32 mm SVL versus 39.48 mm SVL for the unique type of $D$. inexpectatus), undivided or incompletely divided subdigital scansors, and single internasal scale (versus 3 internasals). Unfortunately, the male of $D$. inexpectatus is unknown, so the preanal pore condition for this species is undetermined.

For the seven species for which males are known, three species possess two rows of preanal pores ( $D$. thomaswhitei, $D$. validiclavis, $D$. nehoueensis) and three have only a single row of pores (D. kaalaensis, D. koniambo, D. poumensis). Dierogekko insularis is variable in this regard and may have from zero to eight pores in a posterior row of pores. Although all species are small in absolute terms, they segregate into several categories of maximum body size: $D$. kaalaensis, $D$. thomaswhitei and $D$. validiclavis all reach SVLs of approximately 45 mm . Excluding $D$. inexpectatus (known only from a single specimen), most of the remaining species reach a maximum size of $41-43 \mathrm{~mm}$, whereas D. poumensis, for which a large sample is available, barely exceeds 38 mm SVL. Finally, the species do differ subtly in color pattern, although there is considerable variation in some taxa (see individual species diagnoses and life photographs).

## DISCUSSION

Phylogeny of Dierogekko.- Relationships within Dierogekko are well supported by ND2 sequence data. As expected, the more slowly evolving RAG-1 gene contributes less to intrageneric resolution, but is fully consistent with the ND2 data. The basal division in the genus separates $D$. poumensis from all remaining taxa (Fig. 32). Based on the Bayesian analysis $D$. validiclavis and $D$. inexpectatus are sister species, with $D$. nehoueensis the sister group to this pair. This cluster as a whole forms the sister group to ( $D$. insularis ( $D$. koniambo ( $D$. kaalaensis, $D$. thomaswhitei). Under parsimony $D$. insularis forms a trichotomy with the other two clades in a strict consensus of equally parsimonious trees. Each of the individual species receives strong support (Bayesian posterior probability $1.00,100 \%$ bootstrap support) and all supraspecific groupings, except that clustering $D$. insularis with the Koniambo/Taom/Kaala clade, are supported by posterior probabilities of at least 0.99 . With respect to mainland species, the phylogeny is geographically coherent. The northernmost taxon (D. poumensis) is the sister group to a northern ultramafics plus northeastern (validiclavis sensu stricto) clade plus a southern ultramafic clade.

Within $D$. insularis, the Île Art population is the sister group to that from Île Pott, with Île Yandé outside of this. In other taxa represented by more than one locality ( $D$. kaalaensis, $D$. validiclavis) specimens from each locality are reciproically monophyletic. The exception is $D$. nehoueensis, in which there is almost no differentiation between samples from Néhoué and nearby Tiébaghi.

Age of the Dierogekko radiation.- A comparative analysis of the New Caledonian and New Zealand skink and gecko fauna suggests that all of the within-island speciation in both taxonomic groups occurred approximately 30 million years ago (Jackman, 2005; Jackman and Bauer, in prep), following the maximal extent of the Oligocene marine transgression, which reduced New Zealand to an area of about $18 \%$ of its current aerial land mass (Cooper and Millener 1993). This transgression is believed to have resulted in the Oligocene bottleneck, which reduced genetic and
phyletic diversity in New Zealand and is thought to have been important in the evolutionary history of many animal taxa, including insects, birds, and lizards, at least in New Zealand (Cooper and Cooper 1995; Hickson et al. 2000; Chambers et al. 2001; von Dohlen and Teulon 2003; Trewick and MorganRichards 2005; although its impact on the flora remains to be substantiated, Lee et al. 2001). Comparable influence of Oligocene transgressions on the biotic history of New Caledonia has been suggested (Bauer 1999), but has not been previously demonstrated, and other Tertiary events, particularly the Eocene ophiolitic obduction, have been proposed as important events (Lowry 1998; Lee et al. 2001).

Assuming a 30 million year old time to common ancestry for the most divergent lineages of New Caledonian diplodactylid geckos and using the program r8s to calibrate the ages of divergence for the ND2 data, the estimated time to common ancestry of the genus Dierogekko is 19.2 million years. Using the same calibration, the most recent speciation event in the genus is 5.7 million years. A somewhat independent estimate of the same ages using a rate of $0.65 \%$ change per lineage per million years based on a variety of reptile and amphibian lineages (Macey et al. 1998; Weisrock et al. 2001) gives estimates of 18.6 and 10.1 million years for the age of the genus and the most recent speciation event. As a whole, the Dierogekko clade is roughly the same age as the Bavayia cyclura group, but older than the Bavayia sauvagii group.

These age estimates are in sharp contrast to those found by Murienne et al. (2005) for the New Caledonian cockroach genus Angustonicus. These authors argued that diversification in this lineage was no older than two million years and used this to support a broader hypothesis that the biotic richness and endemism of New Caledonia are not necessarily reflective of a Gondwanan origin of the indigenous taxa. While we agree that much of the modern New Caledonian biota owes its diversification to Tertiary events, we believe that the young age of the Angustonicus radiation is not typical of the fauna as a whole. Rather, our data suggest that events from the mid-Tertiary onwards have played a role in the cladogenesis of the diplodactylid geckos of the region. Although some reconstructions suggest that all of New Caledonia was submerged during the Paleocene (Murienne et al. 2005), thus necessitating a dispersalist origin for all land biota, evidence from the flora suggests that some land area existed even during periods of maximal obduction and transgression (Lowry 1998). Further, rough dating of the divergence between New Caledonian and New Zealand diplodactylids, as well as that between those lineages and Australian diplodactylids, is consistent with cladogenesis associated with Late Cretaceous to Early Tertiary geological events occurring
along the eastern margin of Gondwanaland (Jackman 2005). Thus, we follow Bauer (1990, 1999) in considering the New Caledonian diplodactlyid fauna to be Gondwanan in origin, although it is now clear that the "modern" radiation of taxa is more recent and consistent with the Oligocene bottleneck hypothesis. A similar extinction followed by radiation of remaining taxa has been postulated to explain the history of the New Caledonian flora as well (Jaffré et al. 1987).

Biogeography.- Dierogekko is restricted to the northern portion of New Caledonia and to islands that were once connected to the New Caledonian mainland. Specifically, they occur allopatrically in association with a series of isolated ultramafic massifs northwest of the Grande Terre. This chain of ultramafics extends from the Massif du Boulinda ( 1330 m ) in the south, thorough the Massif de Kopéto ( 1083 m ), the Massif de Koniambo ( 940 m ), the Massif d'OuazangouTaom (1092 m), Mont Kaala (1079 m), Dôme de Tiébaghi (599 m), and Sommet Poum ( 414 m), to the Îles Belep in the far north (Sautter 1981; Jaffré et al. 1987; Morat 1993). Indeed all of the isolated peaks from Koniambo north, except Ouazangou, which has not been sampled, support endemic species of Dierogekko. Only D. validiclavis sensu stricto occurs entirely outside the ultramafic massifs, being restricted to the metamorphic rocks of the Panié Massif in the northeast of New Caledonia. In addition, $D$. nehoueensis occurs in the lowland riverine Néhoué Valley, adjacent to the Dôme de Tiébaghi, where it is present on an alluvial substrate.

Ultramafic rocks include peridotites and serpentinites, which are composed of magnesium silicates containing iron, nickel, cobalt and manganese. They give rise to lateritic soils that are poor in potasium, calcium and phosphorus and rich in heavy metals (Ni, Mn and Co) (Jaffré et al. 1994, Lowry 1998). The ultramafic massifs are substantially drier than the axial ranges of metamorphic rock that parallel them to the east (Paris 1981; Sautter 1981), and they support a rich and distinctive flora (Jaffré 1974; Jaffré and Latham 1974). They are mostly covered by maquis shrubland characterized by evergreen shrubs and also support a high diversity of sedges (Cyperaceae). Elevations above 700 m are typically dominated by species of Costularia, Hibbertia, Knightia, Dicranopteris, Gahnia, and Grevillea (Jaffré 1974; Jaffré and Latham 1974), although small and highly fragmented humid forest patches also remain despite often intensive mining activity. These may be dominated by podocarps or lauraceous trees, or by species of Casuarina, Metrosideros, Nothofagus, or Araucaria (Jaffré 1980; Morat et al. 1986; Jaffré et al. 1987). Plant diversity is especially high in these regions, with more than 1800 species or more than $60 \%$ of the New Caledonian flora. Further, of these, $98 \%$ are New Caledonian endemics and at least 1176 species are restricted to ultramafics. The dominant vegetation in much of the ultramafic regions is maquis vegetation. The maquis has approximately 1150 species, of which almost $90 \%$ are endemic (Jaffré et al. 1994, 2001). More specifically, each of the northwestern ultramafic massifs is associated with endemic plants (Jaffré et al. 1987).

By the late Eocene peridotites, the most widespread of the ultramafic substrates, covered virtually all of New Caledonia (Guillon 1975; Jaffré et al. 1987, 1994). Now they cover much of the southern third of New Caledonia as well as the Île des Pins off the southern coast and numerous northern isolates, including the Belep islands, which together constitute the Ophiolitic Nappe (Cluzel et al. 2001). Ultramafics have been implicated in both the major extinction and subsequent radiation of the flora (Jaffré et al. 1987, 1994). Since the end of the Eocene, erosion has reduced and fragmented this previously continuous substrate (Guillon 1969, 1975; Trescases 1969, 1975; Guillon and Routhier 1971), and it is possible that such fragmentation may be associated with cladogenesis in Dierogekko. However, there have also been significant climatic and vegetational changes in New Caledonia during this period (Lowry 1998; Lee et al. 2001) and specific candidate cladogenetic events remain elusive.

In contrast to earlier interpretations of the New Caledonian fauna (e.g., Diamond 1984), it now
appears that New Caledonia has been the site of numerous in situ radiations of vertebrate taxa (Bauer 1989; Bauer and Sadlier 1993, 2000). Indeed, animals and plants of many groups exhibit significant radiations within New Caledonia (e.g., Haase and Bouchet 1998; Eibl et al. 2001). The fauna of the northwestern ultramafics has been poorly studied to date. Putatively endemic scarabid beetles have ben reported from the Îles Belep (Paulian and Pluot-Sigwalt 1984). Unfortunately, explicit phylogenetic hypotheses are lacking for all of these groups, so it is not yet possible to apply cladisitc biogeographic methods (Humphries and Parenti 1999) to test hypotheses of area relationship among the isolated peaks.

Conservation.- All of the new species of Dierogekko face threats from habitat destruction and from predation or harrasment from introduced animals. Introduced mammals, in particular, have been demonstrated to have negative impacts on the New Caledonian native biota in general (Gargomigny et al. 1996) and most such species have successfully invaded even the most remote, high-elevations of the island (Rouys and Theuerkauf 2003). Rats and cats are the most frequently encountered introduced mammals in Dierogekko habitats. Both have been known to cause local lizard extirpation or to decrease population densities (Whitaker 1978; Newman 1994) and rats may also alter habitats through their differential consumption of seeds and young plants (Campbell and Atkinson 1999, 2002). Habitat destruction or alteration is also caused by deer (Cervus timorensis) and pigs (Sus scrofa), both of which are present at most of the sites where Dierogekko spp. have been collected. The gecko Hemidactylus frenatus has been known to competitively exclude other gecko species in areas where it has been introduced (e.g., Petren et al. 1993, Petren and Case 1996; Cole et al. 2005). Dierogekko spp. populations are presently known to occur syntopically with $H$. frenatus at several localities and they may be a threat to another newly described New Caledonian gecko, Oedodera marmorata (Bauer et al. 2006). Given the successful spread of H. frenatus elsewhere in New Caledonia (Bauer and Sadlier 2000), we consider it a potential threat to those populations of Dierogekko occurring at lower elevations.The fire ant, Wasmannia auropunctata, was encountered sympatrically with only one of the mainland Dierogekko sites (Rivière Néhoué), but it does occur on Yandé and the Îles Beleps, and at Mt. Taom it has been recorded from lower elevations (Whitaker et al. 2004). This invasive species is highly competitive with other ants and is widespread in New Caledonia (Le Breton et al. 2003). It is known to impact negatively native geckos (Jourdan et al. 2001) and must also be considered a potential threat.

Probably the greatest threat to Dierogekko, however, is from wholesale habitat destruction. Although $D$. validiclavis receives a measure of protection on the Massif de Panié, the species occurring in the northwest of New Caledonia are all subject to major habitat alteration, chiefly from mining operations. Operational mines are present on Taom, Kaala, the Dôme de Tiébaghi and Sommet Poum, and a large new mine is planned for Koniambo. Past mining activities have altered landscapes and vegetation at the island localities and wild fires pose a significant threat at all sites (Sadlier et al. 2004: Whitaker et al. 2004). Finally, although the Rivière Néhoué site has some protection as a recreational park, this very use opens the area up to further degradation, both through direct human activity, but also through the intentional or inadvertent introduction of non-native animals, including cattle and fire ants.

We have modified IUCN criteria (1996) for assigning taxa to risk categories, relying on estimated distribution in combination with known or perceived threats, where area of occupancy has been adjusted for the total area of New Caledonia (Sadlier and Bauer 2003; Sadlier et al. 2004). A species represented by 5 or fewer site records ( $2.5 \%$ or less of total landmass, where each site record represents a potential maximum area of $100 \mathrm{~km}^{2}$ and reflects the potential maximum degree of population fragmentation) is considered Endangered dependent upon the degree of fragmentation in the presence of threats to the area of occupancy or extent and quality of habitat. Critically Endangered
species are those known from a single location of $<100 \mathrm{~km}^{2}$ and exposed to diminishing habitat area and/or quality due to actual habitat loss or introduced predators (Sadlier and Bauer 2003; Whitaker et al. 2004). On this basis Dierogekko thomaswhitei, D. kaalaensis, D. poumensis, D. inexpectatus and D. koniambo are Critically Endangered and D. nehoueensis and D. insularis are Endangered. Dierogekko validiclavis, while occurring at only two sites (Mt. Panié and Mt. Mandjélia) is considered Vulnerable rather than Endangered because of the large extent and potential habitat for it that has yet to be surveyed (Sadlier and Bauer 2003).

Whitaker et al. (2004) proposed that protection should be given to all remaining high elevation closed forest patches on ultramafic substrates in New Caledonia and that high elevation maquis should also be considered of high conservation value. They also suggested that mammal eradication programs, such as those implemented successfully in New Zealand (Towns et al. 1997; Towns and Broome 2003) could be put in place for the northern islands of New Caledonia, including île Yandé, Île Art, and Île Pott. While the limited distributions of all species of Dierogekko will always leave them vulnerable to habitat perturbations, actions such as these would do much to decrease risk levels to populations.

The recognition of seven new species and of the distinctiveness of these species as a group from other New Caledonian diplodactylid geckos serves further to highlight both the species richness and phyletic diversity of the New Caledonian herpetofauna. Both of these concepts had been grossly underestimated for many years, due to inadequate collecting and general inattention by systematists (Bauer 1989). Recent intensive work coupled with extensive sampling, and a paradigm shift to lineage-based species concepts (de Queiroz 1998; Brown and Diesmos 2001), have demonstrated that the New Caledonian herpetofauna exhibits a high degree of intra-island or microendemism (Bauer and Sadlier 1993, 2000; Bauer 1999). Specifically, the southern ultramafic block of New Caledonia, along with the Panié massif and several karst areas had been identified as localized areas of reptile endemism. The exploration of the northwestern ultramafic peaks and surrounding areas in northern New Caledonia (Whitaker Consultants Limited 2002; Whitaker et al. 2004) has revealed staggering levels of microendemism, with locally or strictly endemic skinks and/or geckos on each of the ultramafic peaks extending from Boulinda in the south to the Îles Belep in the north. Further endemism has been recognized even from lowland sites in the northwest of the island (Bauer et al. 2006). These results further emphasize the uniqueness and conservation priority of New Caledonia (Myers 1988, 1990; Chazeau 1993; Mittermeier et al. 1996, 1999; Myers et al. 2000; Lowry et al. 2004).

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## Literature Cited

Anderson S., A.T. Bankier , B.G. Barrell, M.H.L. de Bruidn, A.R. Coulson, J. Drouin, I.C. Eperon, D.P. Nierlich, B.A. Roe, F. Sanger, P.H. Schreier, A.J.H. Smith, R. Staden, and I.G. Young. 1981. Sequence and organization of the human mitochondrial genome. Nature 290: 457-465.
BAUER, A.M. 1989. Reptiles and the biogeographic interpretation of New Caledonia. Tuatara 30:39-50.
BaUER, A.M. 1990. Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia: Gekkonidae). Bonner Zoologische Monographien 30:1-220.
BAUER, A. M. 1999. The terrestrial reptiles of New Caledonia: the origin and evolution of a highly endemic herpetofauna. Pages 3-25 in H. Ota, ed., Tropical Island Herpetofauna: Origin, Current Diversity, and Conservation. Elsevier, Amsterdam, Netherlands.
Bauer, A.M., T.R. Jackman, and M. Kiebish. 2004. Molecular systematics of the New Caledonian geckos Rhacodactylus and Eurydactylodes (Squamata: Diplodactylidae). New Zealand Journal of Zoology 31:100.
Bauer, A.M., T. Jackman, R.A. Sadlier, and A.H. Whitaker. 2006. A new genus and species of diplodactylid gecko (Reptilia: Squamata: Diplodactylidae) from northwestern New Caledonia. Pacific Science 60:125-135, 1 pl.
Bauer, A.M., J. Jones, and R.A. Sadlier. 2000. A new high-elevation Bavayia (Reptilia: Squamata: Diplodactylidae) from northeastern New Caledonia. Pacific Science 54:63-69.
Bauer, A.M., and R.A. Sadlier. 1993. Systematics, biogeography and conservation of the lizards of New Caledonia. Biodiversity Letters 1:107-122.
Bauer, A.M., and R.A. Sadlier. 2000. The Herpetofauna of New Caledonia. Society for the Study of Amphibians and Reptiles, Ithaca, New York, USA. xii +310 pp., 24 pls.
Bauer A.M., A.H. Whitaker, and R.A. Sadler. 1998. Two new species of the genus Bavayia (Reptilia: Squamata: Diplodactylidae) from New Caledonia. Pacific Science 52:342-355.
Bergmann, P.J., and A.P. Russell. 2006. Systematics and biogeography of the widespread Neotropical gekkonid genus Thecadactylus (Squamata), with the description of a new cryptic species. Zoological Journal of the Linnean Society. (In press.)
Blaxter, M.L. 2004. The promise of a DNA taxonomy. Philosophical Transactions of the Royal Society of London B 359:669-679.
Brown. R.M., AND A.C. Diesmos. 2001. Application of lineage-based species concepts to oceanic island frog populations: the effects of differing taxonomic philosophies on the estimation of Philippine biodiversity. Silliman Journal 42:133-162.
Campbell, D.J., and I.A.E. Atkinson. 1999. Effects of kiore (Rattus exulans) on recruitment of indigenous coastal trees on northern offshore islands of New Zealand. Journal of the Royal Society of New Zealand 29:265-290.
Campbell. D.J., and I.A.E. Atkinson. 2002. Depression of tree recruitment by the Pacific rat (Rattus exulans Peale) on New Zealand's northern offshore islands of New Zealand. Biological Conservation 107:19-35.
Chambers, G.K.., W.M. Boon. T.R. Buckiey, and R.A. Hitchmough. 2001. Using molecular methods to understand the Gondwanan affinities of the New Zealand biota: three case studies. Australian Journal of Botany 49:377-387.
Chazeau, J. 1993. Research on New Caledonian terrestrial fauna: achievements and prospects. Biodiversity Letters 1:123-129.
Cluzel. D.. J.C. Aitchison, and C. Picard. 2001. Tectonic accretion and underplating of mafic terranes in the Late Eocene intraoceanic fore-arc of New Caledonia (Southwest Pacific): geodynamic implications. Tectonophysics 340:23-59.
Cole. N.C.. C.G. Jones. and S. Harris. 2005. The need for enemy-free space: the impact of an invasive gecko
on island endemics. Biological Conservation 125:467-474.
Conservation International and Mardia Society. 1998. Conserving Biodiversity in Province Nord, New Caledonia. 2 vols. Maruia Society, Conservation International and Assemblée de la Province Nord, Nelson, New Zealand, Washington, D.C. and Koné, New Caledonia. [1] + xxix + 113 pp., i +85 pp.
COOPER, A., AND R.A. COOPER. 1995. The Oligocene bottleneck and New Zealand biota: genetic record of a past environmental crisis. Proceedings of the Royal Society of London B 261:293-302.
Cooper, R.A., and P.R. Millener. 1993. The New Zealand biota: historical background and new research. Trends in Ecology and Evolution 8:429-433.
De Queiroz, K. 1998. The general lineage concept of species, species criteria, and the process of speciation. Pages 57-75 in D.J. Howard and S.H. Berlocher, eds., Endless Forms: Species and Speciation. Oxford University Press, Oxford, UK.
Diamond, J. 1984. Biogeographic mosaics in the Pacific. Pages 1-14 in F.J. Radovsky, P.H. Raven, and S.H. Sohmer, eds., Biogeography of the Tropical Pacific. Bishop Museum Special Publication 72. Honolulu, Hawai' i, USA.
Eibl, J.M., G.M. Plunkett, and P.P. Lowry, II. 2001. Evolution of Polyscias sect. Tieghemopanax (Araliaceae) based on nuclear and chloroplast DNA sequence data. Adansonia, sér. 3, 23:23-48.
Ekstrom, J.M.M., J.P.G. Jones, J. Willis, and I. Isherwood. 2000. The Humid Forests of New Caledonia. Biological Research and Conservation Recommendations for the Vertebrate Fauna of Grande Terre. CSB Conservation Publications, London, UK. (6) $+94+(13) \mathrm{pp}$.
Ereshefsky, M., ed. 1992. The Units of Evolution; Essays on the Nature of Species. Massachusetts Institute of Technology Press, Cambridge, Massachusetts, USA. xvii + 405 pp.
Ferguson, J.W.H. 2002. On the use of genetic divergence for identifying species. Biological Journal of the Linnean Society 75:509-516.
Gargominy, O., P. Bouchet, M. Pascal, T. Jaffré, and J.-C. Tourneur. 1996. Conséquences des introductions d'espèces animales et végétales sur la biodiversité en Nouvelle-Calédonie. Revue d'Ecologie - La Terre et la Vie 51:375-402.
Good, D.A., A.M. Bauer, and R.A. Sadlier. 1997. Allozyme evidence for the phylogeny of giant New Caledonain geckos (Squamata: Diplodactylidae: Rhacodactylus), with comments on the status of R. leachianus henkeli. Australian Journal of Zoology 45:317-330.
Glillon, J.H. 1969. Données nouvelles sur la composition et la structure du grand massif péridotitique du sud de la Nouvelle-Calédonie. Cahiers ORSTOM, série Géologie 1:7-25.
Guillon, J.H. 1975. Les massifs péridotitiques de Nouvelle-Calédonie. Mémoires ORSTOM 76:1-20.
Glillon, J.H., And P. Routhier. 1971. Les stades d'évolution et de mise en place des massifs ultrabasiques de Nouvelle-Calédonie. Bulletin du Bureau de Recherches Géologiques et Minières, série 2, section IV, 2:5-38.
HAASE, M., AND P. Bouchet. 1998. Radiation of crenobiontic gastropods on an ancient continental island: the Hemistomia-clade in New Caledonia (Gastropoda: Hydrobiidae). Hydrobiologia 367:43-129.
Han, D., K. Zhou, and A.M. Bauer. 2004. Phylogenetic relationships among gekkotan lizards inferred from C-mos nuclear DNA sequences and a new classification of the Gekkota. Biological Journal of the Linnean Society 83:353-368.
Hebert, P.D.N., A. Cywinska, S.L. Ball, and J.R. deWaard. 2003. Biological identifications through DNA barcodes. Proceedings of the Royal Society of London B 270:33-321.
Henkel, W., AND W. Böhme. 2001. A new carphodactyline gecko of the New Caledonian genus Eurydactylodes (Sauria: Gekkonidae). Salamandra 37:149-156.
Hickson, R.E., K.E. Slack, and P. Lockhart. 2000. Phylogeny recapitulates geography, or why New Zealand has so many species of skinks. Biological Journal of the Linnean Society 70:415-433.
Hollingsworth, B.D. 1998. The systematics of chuckwallas (Sauromalus) with a phylogenetic analysis of other iguanid lizards. Herpetological Monographs 12:38-191.
Holloway, J.D. 1979. A Survey of the Lepidoptera, Biogeography and Ecology of New Caledonia. Dr. W. Junk, The Hague, Netherlands. xii +599 pp.
Howard, D.J., and S.H. Berlocher, eds. 1998. Endless Forms: Species and Speciation. Oxford University Press, New York, New York, USA. 278 pp.

Huelsenbeck, J. P., and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. Bioinformatics 17:754-755.
Humphries, C.J., and L.R. Parenti. 1999. Cladistic Biogeography, $2^{\text {nd }}$ edition. Oxford University Press, Oxford, UK. xi +187 pp .
IUCN. 1996. IUCN Red List of Threatened Animals. The IUCN Species Survival Commission, International Union for Conservation of Nature and Natural Resources. Gland, Switzerland. 368 pp +10 annexes.
Jackman, T. 2005. Tempo and mode of diversification of endemic New Caledonian lizards. Abstracts, 2005 Joint Meeting of Ichthyologists and Herpetologists, Tampa, Florida:243.
Jackman, T.R., A.M. Bauer, and M. Kiebish. 2004. Molecular systematics of the New Caledonian forest geckos (Diplodactylidae: Bavayia). New Zealand Journal of Zoology 31:105.
Jaffré, T. 1974. La végétation et la flore d'un massif de roches ultrabasiques de Nouvelle-Calédonie: le Koniambo. Candollea 29:427-456, 3 pls.
Jaffré, T. 1980. Étude écologique du peuplement vegetal des sols derivés de roches ultrabasiques en Nouvelle-Calédonie. Travaux et Documents de l'ORSTOM 124:1-274.
Jaffré, T., P. Bouchet, and J.M. Veillon. 1998. Threatened plants of New Caledonia: is the system of protected areas adequate? Biodiversity and Conservation 7:109-135.
JAFFRÉ, T., AND M. LATham. 1974. Contribution à l'étude des relations sol-végétation sur un massif des roches ultrabasiques de la côte Ouest de la Nouvelle-Calédonie: le Boulinda. Adansonia, série 2, 14:311-336, 4 folding pls.
Jaffré, T., P. Morat, and J.-M. Veillon. 1994. La flore. Caractéristiques et composition floristique des principales formations végétales. Bois er Forêt des Tropiques, N ${ }^{\circ} 242$ (4e trim.):7-30.
Jaffré, T., P. Morat, J.-M. Veillon, and H.S. MacKee. 1987. Changements dans la vegetation de la Nouvelle-Calédonie au cours du Tertiaire: la vegetation et la flore des roches ultrabasiques. Bulletin du Muséum National d'Histoire Naturelle, Paris, 4 e série, section B, Adansonia 9:365-391.
Jaffré T., P. Morat, J.M. Velllon, F. Rigault, and G. Dagostini. 2001. Composition et Caractérisation de la Flore Indigène de la Nouvelle-Calédonie / Composition and Characterisation of the Native Flora of New Caledonia. Centre IRD de Nouméa (Documents Scientifiques et Techniques, II, 4), Nouméa, New Caledonia. 121 pp., 16 pls.
Jouan, H. 1863. Sur quelques animaux observés à la Nouvelle-Calédonie pendant les années 1861 et 1862. Mémoires de la Société des Sciences Naturelles de Cherbourg 9:89-127.
Jouan, H. 1864. Additions à la faune de la Nouvelle-Calédonie. Mémoires de la Société des Sciences Naturelles de Cherbourg 10:301.
Jourdan, H., R.A. Sadlier, and A.M. Baver. 2000. Premières observations sur les consequences de l'invasion de Wasmannia auropunctata 1863 (Roger) sur les prédateurs superieurs dans les ecosystemes néocalédoniens. Actes des Colloques Insectes Sociaux 13:121-126.
Jourdan, H., R.A. Sadlier, And A.M. Bauer. 2001. Little fire ant invasion (Wasmannia auropunctata) as a threat to New Caledonian lizards: evidences from the sclerophyll forest (Hymenoptera: Formicidae). Sociobiology 38:283-301.
Kluge, A.G. 1967. Higher taxonomic categories of gekkonid lizards and their evolution. Bulletin of the American Museum of Natural History 135:1-60, pls. 1-5.
Kluge, A.G. 1987. Cladistic relationships in the Gekkonoidea (Squamata, Sauria). Miscellaneous Publications, Museum of Zoology, University of Michigan (173):i-iv +1-54.
Le Breton. J., J. Chazeau, A.id H. Jolrd.a.. 2003. Immediate impacts of invasion by Wasmannia auropunctata (Hymenoptera: Formicidae) on native litter ant fauna in a New Caledonian rain forest. Austral Ecology 28:204-209.
Lee, D.E., W.G. Lee, adid N. Mortimer. N. 2001. Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeogeography and climate. Australian Journal of Botany 49:341-356.
Lowry. P.P.. II. 1998. Diversity, endemism, and extinction in the flora of New Caledonia: a review. Pages 181-206 in C.-I. Peng and P.P. Lowry. II. eds.. Threatened and Endangered Floras of Asia and the Pacific Rim. Academia Sinica Monograph Series No. 16, Taipei, Taiwan.
Lowri: P.P. II. J. Mùzinger. P. Bolchet. H. Géralx. A.M. Baler, O. Langrand, and R.A. Mittermeier.
2004. New Caledonia. Pages 192-197 in R.A. Mittermeier, P.R. Gil, M. Hoffmann, J. Pilgrim, T Brooks, C.G. Mittermeier, J. Lamoreux, and G.A.B. Da Fonseca, eds., Hotspots Revisited. CEMEX, Mexico City, Mexico.
Macey, J.R., A. Larson, N.B. Ananjeva, Z. Fang, and T. J. Papenfuss. 1997. Two novel gene orders and the role of light-strand replication in rearrangement of the vertebrate mitochondrial genome. Molecular Biology and Evolution 14: 91-104.
Macey, J. R., J.A. Schulte, II, N.B. Ananjeva, A. Larson, N. Rastegar-Pouyani, S.M. Shammakov, and T.J. Papenfuss. 1998. Phylogenetic relationships among agamid lizards of the Laudakia caucasia species group: testing hypotheses of biogeographic fragmentation and an area cladogram for the Iranian Plateau. Molecular Phylogenetics and Evolution 10:118-131.
Maniatis, T. E.F. Fritsch, and J. Sambrook. 1982. Molecular Cloning: A Laboratory Manual. Cold Spring Harbor Laboratory, Cold Spring Harbor, New York, New York, USA. x + 545 pp.
MAYDEN, R.L. 1997. A hierarchy of species concepts: the denouement in the saga of the species problem. Pages 381-424 in M.F. Claridge, H.A. Dawah and M.R. Wilson, eds., Species: The Units of Biodiversity. Chapman and Hall, New York, New York, USA.
Mickevich, M. F., and J.S. Farris. 1981. The implications of congruence in Menidia. Systematic Zoology 30:351-370.
Mittermeier, R.A., P. Bouchet, A.M. Bauer, T. Werner, and A. Lees. 1999. New Caledonia. Pages 366-377 in R.A. Mittermeier, N. Myers and C.G. Mittermeier, eds., Hotspots: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions. CEMEX, Mexico City, Mexico.
Mittermeier. R.A., T.B. Werner, And A. Lees. 1996. New Caledonia - a conservation imperative for an ancient land. Oryx 30:104-112.
Morat, P. 1993. Our knowledge of the flora of New Caledonia: endemism and diversity in relation to vegetation types and substrates. Biodiversity Letters 1:72-81.
Morat, P., T. Jaffré, J.-M. Veillon, and H.S. MacKee. 1986. Affinités floristiques et considérations sur l'origine des maquis miniers de la Nouvelle-Calédonie. Bulletin du Muséum National d'Histoire Naturelle, Paris, 4 e série, section B, Adansonia 2:133-182.
Murienne, J., P. Grandcolas, M.D. Piulach, X. Bellés, C. D’Haese, F. Legendre, R. Pellens, and E. Gltlbert. 2005. Evolution on a shaky piece of Gondwana: is local endemism recent in New Caledonia? Cladistics 21:2-7.
MyERS, N. 1988. Threatened biotas: "hot spots" in tropical forests. The Environmentalist 8:187-208.
Myers, N. 1990. The biodiversity challenge: expanded hot-spot analysis. The Environmentalist 10:243-256.
Myers, N., R.A. Mittermeier, C.G. Mittermeier, G.A.B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853-858.
Newman, D.G. 1994. Effects of a mouse, Mus musculus, eradication programme and habitat change on lizard populations of Mana Island, New Zealand, with special reference to McGregor's skink, Cyclodina macgregori. New Zealand Journal of Zoology 21:443-456.
Otte, D., And J.A. Endler, eds. 1989. Speciation and its Consequences. Sinauer and Associates, Sunderland, Massachusetts, USA. xiii +679 pp .
Parcher, S.R. 1974. Observations on the natural histories of six Malagasy Chamaeleontidae. Zeitschrift für Tierpsychologie 34:500-523.
Paris, J.P. 1981. Géologie de la Nouvelle-Calédonie. Mémoires du Bureau de Recherches Géologiques et Minières 113:1-278, 2 separate maps.
Paulian, R., and D. Pluot-Sigwalt. 1984. Les canthonines de Nouvelle-Calédonie (Coleoptera, Scarabaeidae). Étude systématique et biogéographique. Bulletin du Muséum National d'Histoire Naturelle, Paris, 4 e série, section A, 6:1091-1133.
Petren, K., D.T. Bolger, and T.J. Case. 1993. Mechanisms in the competitive success of an invading sexual gecko over an asexual native. Science 259:354-358.
Petren; K., and T.J. Case. 1996. An experimental demonstration of exploitation competition in an ongoing invasion. Ecology 77:118-132.
Posada, D., and K.A. Crandall. 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14:817-818.

Roux, J. 1913. Les reptiles de la Nouvelle-Calédonie et des Îles Loyalty. Pages 79-160, pls. 4-5 in F. Sarasin and J. Roux, eds., Nova Caledonia, Zoologie. C.W. Kreidels Verlag, Wiesbaden, Germany.
Rouys, S., and J. Theuerkauf. 2003. Factors determining the distribution of introduced mammals in nature reserves of the southern province, New Caledonia. Wildlfe Research 30:187-191.
Russell, A.P., and A.M. Bauer. 2002. Underwood's Classification of the Geckos: A 21st Century Appreciation. Bulletin of the Natural History Museum, London (Zoology) 68:113-121.
Sadlier R.A. 1989. Bavayia validiclavis and Bavayia septuiclavis, two new species of gekkonid lizard from New Caledonia. Records of the Australian Museum 40:365-370.
Sadlier R.A., and A.M. Bauer. 2003. Conservation status of endemic New Caledonian lizards - an assessment of the distribution and threats to the species of lizard endemic to New Caledonia. http://www.amonline.net.au/herpetology/research/lizards_conservation _intro.htm.
Sadlier, R.A., S.A. Smith, and A.M. Bauer. 2006. A new genus for the New Caledonian scincid lizard Lygosoma euryotis Werner 1909, and the description of a new species. Records of the Australian Museum 58:19-28.
Sadlier, R.A, S.A. Smith, A.M. Bauer, and A.H. Whitaker. 2004. A new genus and species of live-bearing scincid lizard (Reptilia: Scincidae) from New Caledonia. Journal of Herpetology 38:117-127.
Sautter, G., coord. 1981. Atlas de la Nouvelle Calédonie et Dépendances. ORSTOM, Paris. [118] pp., 53 maps, 1 acetate overlay.
Schröder, E., and B. Röll. 2002. Eurydactylodes agricolae Henkel \& Böhme. Sauria, Supplement 24(3):551-554.
Seipr, R., and F.W. Henkel. 2000a. Rhacodactylus, Biologie, Haltung und Zucht. Edition Chimaira, Frankfurt-am-Main, Germany. 173 pp.
Seipp, R., and F.W. Henkel. 2000b. Rhacodactylus, Biology, Natural History and Husbandry. Edition Chimaira, Frankfurt-am-Main, Germany. 173 pp.
Sites, J.W., Jr., and J.C. Marshall. 2003. Delimiting species: a Renaissance issue in systematic biology. Trends in Ecology and Evolution 18:462-470.
Sites, J.W., Jr., and J.C. Marshall. 2004. Operational criteria for delimiting species. Annual Review of Ecology and Systematics 35:199-227.
SWofford, D.L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (* and other methods), version 4b10. Sinauer Associates, Sunderland, Massachusetts, USA.
Towns, D., And K.G. Broome. 2003. From small Maria to massive Campbell: forty years of rat eradication from New Zealand islands. New Zealand Journal of Zoology 30:377-398.
Towns, D., D. Simberloff, and I.A.E. Atkinson. 1997. Restoration of New Zealand islands: redressing the effects of introduced species. Pacific Conservation Biology 3:99-124.
Trescases, J.J. 1969. Premières observations sur l'altération des péridotites en Nouvelle-Calédonie. Pédologie, Géochimie, Géomorphologie. Cahiers ORSTOM, série Géologie 1:27-57.
Trescases, J.J. 1975. L'évolution géochimique supergène des roches ultrabasiques en zone tropicale. Mémoires ORSTOM 78:1-259.
Trewick, S.A., and M. Morgan-Richards. 2005. After the deluge: mitochondrial DNA indicates Miocene radiation and Pliocene adaptation of tree and giant weta (Orthoptera: Anostostomatidae). Journal of Biogeography 32:295-309.
Underwood, G. 1954. On the classification and evolution of geckos. Proceedings of the Zoological Society of London 124:469-492.
Underwood, G. 1955. Classification of geckos. Nature 175:1089-1090
Veillon, J.-M.. G. Dagostini. and T. Jaffré. 1999. Étude de la forêt sclérophylle de la Province Nord en Nouvelle-Calédonie. Conventions Sciences de la Vie Botanique N ${ }^{\circ}$ 10. Centre IRD, Nouméa, New Caledonia. 54 pp.
Virot, R. 1956. La végetation canaque. Mémoires du Muséum National d'Histoire Naturelle, n.s., B 7:1-398.
von Dohlen. C.D.. and D.A. Teulon. 2003. Phylogeny and historical biogeography of New Zealand indigenous Aphidini aphids (Hemiptera. Aphididae): an hypothesis. Annals of the Entomological Society of America 96:107-116.
WATSON. D.M. 2005. Diagnosable versus distinct: evaluating species limits in birds. BioScience 55:60-68.

Weisrock, D.W., J.R. Macey, I.H. Ugurtas, A. Larson, and T.J. Papenfuss. 2001 Molecular phylogenetics and historical biogeography among salamandrids of the 'true' salamander clade: rapid branching of numerous highly divergent lineages in Mertensiella luschani associated with the rise of Anatolia. Molecular Phylogenetics and Evolution 18:434-448.
Whitaker, A.H. 1978. The effects of rodents on reptiles and amphibians. Pages $75-88$ in P.R. Dingwall, I.A.E. Atkinson and C. Hay, eds., The Ecology and Control of Rodents in New Zealand Nature Reserves. New Zealand Department of Lands and Survey Information Series No. 4, Wellington, New Zealand. 237 pp.
Whitaker, A.H., R.A. Sadlier, A.M. Bauer, and V.A. Whitaker. 2004. Biodiversity and Conservation Status of Lizards in Threatened and Restricted Habitats of North-Western New Caledonia. Report by Whitaker Consultants Limited to Direction du Développement Économique et de l’Environnement, Province Nord, Koné, New Caledonia. vi + 105 pp.
Whitaker Consultants Limited. 2002. Biodiversity and Conservation Status of Lizards in Threatened and Restricted Habitats of North-western New Caledonia: Report of the First Field Mission, SeptemberOctober 2001. Unpublished report to Direction du Développement conomique et de l'Environnement, Province Nord, Koné, New Caledonia. iii +29 pp.
Wiens, J.J., and T.A. Penkrot. 2002. Delimiting species using DNA and morphological variation and discordant species limits in spiny lizards (Sceloporus). Systematic Biology 51:69-91.
Wievs, J.J., and M.R. Servedio. 2000. Species delimitation in systematics: inferring diagnostic differences between species. Proceedings of the Royal Society of London B 267:631-636.
Wright, J.L. 1999. The Phylogeny of Bavayia (Reptilia: Diplodactylidae) Based on Mitochondrial DNA, Allozymes and Morphological Evidence, Including the Description of Two New Species. M.S. Thesis, Villanova University, Villanova, Pennsylvania, USA. xi + 133 pp.
Wright, J.L., A.M. Bauer. and R.A. Sadlier. 2000. Two New Gecko Species Allied to Bavayia sauvagii and Bavavia cyclura (Reptilia: Squamata: Diplodactylidae) from New Caledonia. Pacific Science 54:39-55.

Table 1. Primers used in this study. Primers are designated by their 3' ends, which correspond to the position in the human mitochondrial genome (Anderson et al. 1981). H and L designate primers whose extension produces the heavy and light strands, respectively.

| Human <br> position | Gene | Sequence | Reference |
| :--- | :---: | :--- | :--- |
| L4419 | tRNAMet 5'-AAGCAATTGGGCTCATACC-3' | Macey et al. (1997) |  |
| L5002 | ND2 | 5' CAAACACAAACCCGRAAAAT-3' | This Study |
| H5140 | ND2 | 5'-CCYAGGTCTAAGAGGGTTTTTG-3' | This Study |
| H5617b | tRNAAla | 5'-CTGAATGCAACTCAGACACTTT-3' | Macey et al. (1997) |
| H5934 | COI | 5'-AGRGTGCCAATGTCTTTGTGRTT-3' | Macey et al. (1997) |

Table 2. Museum Vocher Numbers and Corresponding GenBank accession numbers.

| Species | Museum Voucher Number | Genbank Locality |
| :---: | :---: | :---: |
| Dierogekko poumensis | AMS R 161205 | Sommet Poum |
| Dierogekko poumensis | CAS 231860 | Sommet Poum |
| Dierogekko poumensis | CAS 231861 | Sommet Poum |
| Dierogekko nehoueensis | AMS R 161242 | Dôme de Tiébaghi |
| Dierogekko nehoueensis | AMS R 166970 | Rivière Néhoué |
| Dierogekko nehoueensis | CAS 231855 | Rivière Néhoué |
| Dierogekko inexpectatus | MNHN 2004.0025 | Sommet Poum |
| Dierogekko validiclavis | AMS R 149305 | Mt. Panié |
| Dierogekko validiclavis | AMS R 144230 | Mt. Panié |
| Dierogekko validiclavis | AMS R 153696 | Mt. Mandjélia |
| Dierogekko validiclavis | AMS R 153695 | Mt. Mandjélia |
| Dierogekko koniambo | CAS 231873 | Mt. Koniambo |
| Dierogekko thomaswhitei | AMS R 161153 | Mt. Taom |
| Dierogekko thomaswhitei | CAS 231876 | Mt. Taom |
| Dierogekko kaalaensis | CAS 231872 | Piton de Pandop |
| Dierogekko kaalaensis | CAS 231870 | Kaala |
| Dierogekko kaalaensis | MNHN 2004.0017 | Kaala |
| Dierogekko insularis | CAS 231857 | İle Yandé |
| Dierogekko insularis | AMS R 166972 | Île Yandé |
| Dierogekko insularis | CAS 231858 | Île Yandé |
| Dierogekko insularis | AMS R 166974 | Île Yandé |
| Dierogekko insularis | AMS R 161070 | İle Art |
| Dierogekko insularis | MNHN 2003.0020 | Île Art |
| Dierogekko insularis | CAS 231865 | Ile Pott |
| Dierogekko insularis | AMS R 161067 | Île Pott |
| Oedodera marmorata | AMS R 161254 | Creek à Paul. Sommet Noir, Paagoumène |
| Pseudothecadactrlus lindneri | AMS R 90195 | Liverpool River, Northern Territory, Australia |

Table 3. Mensural data for the types of Dierogekko koniambo, sp. nov. Abbreviations as in Materials and methods. All measurements in mm.

|  | MNHN | AMS R | AMS R | AMS R | CAS | CAS | CAS |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 2004.0016 | 161114 | 161130 | 161131 | 231873 | 231874 | 231875 |
|  | Holotype | Paratype | Paratype | Paratype | Paratype | Paratype | Paratype |
| Sex | male | male | male | female | female | male | male |
| SVL | 42.6 | 43.0 | 41.8 | 42.2 | 41.9 | 40.9 | 43.0 |
| ForeaL | 4.8 | 5.2 | 5.4 | 5.2 | 5.1 | 5.2 | 4.9 |
| CrusL | 6.2 | 5.8 | 5.5 | 5.9 | 6.0 | 5.9 | 5.8 |
| TailL | 40.8 | 31.1 | 33.0 | 33.6 | 35.3 | 4.0 | 42.8 |
| $\quad$ (regen.) | 23.5 | 28.1 | 29.8 | 31.0 | 31.9 | broken | 27.2 |
| TailW | 5.0 | 5.4 | 4.2 | 5.3 | 5.5 | N/A | 4.4 |
| TrunkL | 18.1 | 19.1 | 16.2 | 18.6 | 18.8 | 19.0 | 18.7 |
| HeadL | 12.2 | 11.3 | 11.2 | 12.1 | 11.0 | 11.2 | 11.2 |
| HeadW | 7.2 | 7.9 | 7.4 | 7.6 | 7.4 | 7.4 | 7.2 |
| HeadH | 5.0 | 4.2 | 4.2 | 4.2 | 5.0 | 4.5 | 4.1 |
| OrbD | 3.1 | 2.8 | 2.8 | 2.7 | 2.8 | 3.0 | 2.8 |
| EyeEar | 3.2 | 3.1 | 3.0 | 3.0 | 2.7 | 2.8 | 2.4 |
| SnEye | 4.8 | 4.6 | 4.4 | 4.1 | 4.4 | 4.4 | 4.3 |
| NarEye | 3.0 | 2.8 | 3.0 | 2.6 | 2.7 | 3.1 | 2.6 |
| Interorb | 4.2 | 4.1 | 3.8 | 4.0 | 3.8 | 4.0 | 3.7 |
| EarL | 1.5 | 1.4 | 1.4 | 1.3 | 1.3 | 1.3 | 1.5 |
| Internar | 1.7 | 1.8 | 1.5 | 1.5 | 1.7 | 1.6 | 1.9 |

Table 4. Mensural data for the types of Dierogekko kaalaensis, sp. nov. Abbreviations as in Materials and methods. All measurements in mm.

|  | MNHN | AMS R | AMS R | CAS | CAS | CAS |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 2004.0017 | 161097 | 161098 | 231870 | 231871 | $23 i i$ |
|  | Holotype | Paratype | Paratype | Paratype | Paratype | Paratype |
| Sex | male | female | male | male | female | female |
| SVL | 42.2 | 45.4 | 42.0 | 41.7 | 33.4 | 40.7 |
| ForeaL | 5.4 | 5.3 | 4.8 | 5.1 | 4.3 | 5.0 |
| CrusL | 6.4 | 6.1 | 5.9 | 6.1 | 5.1 | 5.8 |
| TailL | 41.8 | 42.6 | 45.5 | 49.0 | 30.0 | 38.6 |
| $\quad$ (regen.) | 30.4 | 31.3 | 24.4 | 12.9 | 22.8 | 10.3 |
| TailW | 5.4 | 5.5 | 4.1 | 4.4 | 3.4 | 4.8 |
| TrunkL | 15.9 | 18.2 | 14.8 | 16.7 | 14.0 | 16.2 |
| HeadL | 11.6 | 11.9 | 12.2 | 12.7 | 10.8 | 11.7 |
| HeadW | 8.1 | 8.0 | 7.8 | 7.8 | 6.5 | 7.6 |
| HeadH | 4.0 | 4.3 | 4.5 | 4.1 | 3.5 | 3.9 |
| OrbD | 2.6 | 3.1 | 3.2 | 2.7 | 2.5 | 3.0 |
| EyeEar | 3.0 | 2.9 | 2.6 | 2.9 | 2.8 | 2.6 |
| SnEye | 4.3 | 4.3 | 4.3 | 4.3 | 3.8 | 4.2 |
| NarEye | 2.9 | 3.0 | 2.6 | 3.0 | 2.5 | 2.8 |
| Interorb | 3.8 | 3.8 | 3.4 | 3.7 | 3.4 | 4.0 |
| EarL | 1.6 | 1.3 | 1.5 | 1.5 | 1.4 | 1.4 |
| Internar | 1.4 | 1.3 | 1.5 | 1.6 | 1.3 | 1.2 |

Table 5. Mensural data for the types of Dierogekko thomaswhitei, sp. nov. Abbreviations as in Materials and methods. All measurements in mm.

|  | MNHN | AMS R | AMS R | AMS R AMS R | CAS | CAS | CAS | CAS |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 2004.0018 | 166975 | 161153 | 161178 | 161180 | 231837 | 231838 | 231876 | 231877 |
|  | holotype | paratype | paratype | paratype | paratype | paratype | paratype | paratype paratype |  |
| Sex | male | male | male | male | female | male | juv. female | female | male |
| SVL | 41.7 | 40.8 | 41.9 | 42.6 | 44.9 | 38.3 | 33.6 | 43.6 | 43.4 |
| ForeaL | 5.4 | 4.8 | 5.6 | 5.4 | 5.6 | 4.8 | 4.4 | 5.3 | 4.9 |
| CrusL | 5.8 | 6.0 | 6.4 | 6.4 | 6.3 | 5.4 | 5.0 | 6.1 | 5.6 |
| TailL | 39.0 | 19.0 | 33.2 | 37.7 | 38.4 | 45.4 | 34.4 | 38.7 | 39.3 |
| $\quad$ (regen.) | 23.4 | broken | 19.6 | 32.1 | 33.5 | 14.8 | 6.4 | 27.3 | 27.3 |
| TailW | 4.0 | 4.4 | 5.1 | 4.8 | 5.2 | 4.0 | 3.3 | 5.0 | 4.9 |
| TrunkL | 15.8 | 17.3 | 18.5 | 18.8 | 18.6 | 15.7 | 13.9 | 18.4 | 17.7 |
| HeadL | 12.6 | 11.0 | 12.0 | 12.0 | 12.5 | 11.7 | 9.5 | 11.5 | 11.9 |
| HeadW | 8.0 | 7.3 | 7.5 | 7.1 | 8.0 | 6.9 | 6.1 | 7.3 | 7.2 |
| HeadH | 4.8 | 4.7 | 4.8 | 5.1 | 5.9 | 4.8 | 3.8 | 4.7 | 4.5 |
| OrbD | 2.8 | 2.8 | 2.8 | 2.5 | 3.2 | 2.5 | 2.2 | 3.0 | 2.9 |
| EyeEar | 3.0 | 3.0 | 2.6 | 3.0 | 3.0 | 3.0 | 2.7 | 2.7 | 2.6 |
| SnEye | 4.2 | 4.3 | 4.6 | 4.7 | 4.8 | 3.8 | 3.6 | 4.6 | 4.5 |
| NarEye | 2.9 | 2.7 | 2.8 | 3.2 | 2.9 | 2.6 | 2.5 | 2.9 | 3.0 |
| Interorb | 3.6 | 3.5 | 3.8 | 3.6 | 3.6 | 3.1 | 2.8 | 3.9 | 3.7 |
| EarL | 1.6 | 1.4 | 2.0 | 1.9 | 2.2 | 1.2 | 1.8 | 1.7 | 1.8 |
| Internar | 1.5 | 1.5 | 1.6 | 1.4 | 1.6 | 1.2 | 1.1 | 1.4 | 1.3 |

Table 6. Mensural data for the types of Dierogekko nehoueensis, sp. nov. Abbreviations as in Materials and methods. All measurements in mm.

|  | MNHN | AMS R | AMS R | AMS R | AMS R | CAS | CAS | CAS | CAS | CAS |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 2004.0019 | 161242 | 161243 | 161244 | 166976 | 231837 | 231838 | 231855 | 231863 | 231864 |
|  | holotype | paratype paratype | paratype | paratype | paratype | paratype | paratype | paratype paratype |  |  |
| Sex | male | female | female | female | female | female | male | female | male | female |
| SVL | 40.3 | 39.9 | 39.4 | 35.1 | 40.0 | 38.1 | 40.2 | 32.4 | 38.5 | 36.0 |
| ForeaL | 5.3 | 4.9 | 5.3 | 4.8 | 5.1 | 5.3 | 4.6 | 4.5 | 4.8 | 4.7 |
| CrusL | 6.1 | 6.0 | 6.0 | 5.1 | 6.3 | 6.0 | 5.6 | 4.7 | 5.5 | 5.6 |
| TailL | 36.2 | 29.5 | 5.5 | 37.2 | 40.0 | 43.4 | 42.7 | 37.6 | 37.8 | 31.1 |
| $\quad$ (regen.) | 32.1 | 27.2 | broken | 17.8 | 14.9 | N/A | N/A | 11.4 | 28.2 | 21.4 |
| TailW | 4.7 | 4.9 | N/A | 4.0 | 3.7 | 3.4 | 4.4 | 4.1 | 4.4 | 3.7 |
| TrunkL | 17.4 | 15.8 | 15.7 | 14.5 | 17.4 | 15.4 | 15.2 | 13.8 | 17.2 | 16.7 |
| HeadL | 12.5 | 11.6 | 10.6 | 10.4 | 11.6 | 10.1 | 12.1 | 9.8 | 11.8 | 10.0 |
| HeadW | 7.3 | 6.7 | 6.4 | 5.6 | 6.7 | 6.1 | 7.3 | 6.2 | 7.3 | 6.0 |
| HeadH | 5.0 | 4.9 | 4.7 | 3.6 | 4.4 | 4.6 | 4.5 | 4.3 | 4.5 | 4.7 |
| OrbD | 2.7 | 2.8 | 2.6 | 2.5 | 2.6 | 2.5 | 2.6 | 2.2 | 2.7 | 2.7 |
| EyeEar | 3.2 | 2.8 | 2.5 | 2.4 | 3.1 | 2.8 | 3.4 | 2.5 | 2.5 | 2.6 |
| SnEye | 4.2 | 4.1 | 3.9 | 3.5 | 4.2 | 3.9 | 4.1 | 3.6 | 4.2 | 3.7 |
| NarEye | 3.3 | 2.7 | 2.7 | 2.5 | 3.2 | 2.6 | 2.8 | 2.4 | 2.8 | 2.5 |
| Interorb | 4.0 | 3.7 | 3.2 | 3.5 | 3.1 | 3.0 | 3.5 | 3.0 | 3.5 | 3.3 |
| EarL | 1.2 | 1.5 | 1.4 | 1.4 | 1.5 | 1.1 | 1.3 | 1.2 | 1.4 | 1.3 |
| Internar | 1.3 | 1.7 | 1.1 | 1.2 | 1.4 | 1.3 | 1.4 | 1.3 | 1.6 | 1.6 |

Table 7. Mensural data for the types of Dierogekko insularis, sp. nov. Abbreviations as in Materials and methods. All measurements in mm.

|  | MNHN2004.0020holotype | AMS R | AMS R | AMS R | AMS R | CAS | CAS | CAS | CAS | CAS |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 161067 | 161073 | 161075 | 166971 | 231858 | 231859 | 231865 | 231867 | 231868 |
|  |  | paratype | paratype | paratype | paratype | paratype | paratype | paratype | paratype | paratype |
| Sex | male | male | male | male | female | male | female | male | male | male |
| SVL | 41.4 | 37.3 | 40.0 | 39.3 | 39.9 | 36.7 | 35.3 | 38.6 | 37.3 | 37.3 |
| ForeaL | 5.5 | 4.9 | 4.8 | 4.6 | 4.3 | 4.4 | 4.0 | 4.7 | 4.9 | 4.7 |
| CrusL | 5.8 | 5.4 | 5.3 | 5.7 | 5.4 | 5.2 | 4.9 | 5.8 | 5.8 | 5.3 |
| TailL | 49.6 | 36.9 | 23.8 | 34.6 | 2.9.0 | 33.5 | 11.6 | 30.1 | 35.8 | 38.6 |
| (regen.) | 19.8 | 18.0 | 21.5 | 31.0 | broken | 17.6 | broken | 3.6 | 24.4 | 16.6 |
| TailW | 4.7 | 4.4 | 3.6 | 4.9 | N/A | 4.5 | 4.7 | 4.4 | 4.6 | 4.3 |
| TrunkL | 16.5 | 15.7 | 14.9 | 18.7 | 17.4 | 14.8 | 15.2 | 16.1 | 14.8 | 13.2 |
| HeadL | 11.1 | 10.4 | 11.0 | 10.6 | 11.7 | 10.5 | 9.8 | 10.4 | 10.8 | 10.3 |
| HeadW | 7.7 | 6.6 | 7.2 | 7.2 | 6.4 | 7.3 | 6.3 | 6.4 | 7.1 | 7.0 |
| HeadH | 4.5 | 4.2 | 4.9 | 4.9 | 4.1 | 4.1 | 4.1 | 4.9 | 4.7 | 5.0 |
| OrbD | 3.0 | 2.6 | 2.9 | 2.8 | 2.7 | 2.6 | 2.5 | 2.9 | 2.7 | 2.6 |
| EyeEar | 3.0 | 3.0 | 3.2 | 3.1 | 3.0 | 2.8 | 2.8 | 2.8 | 2.9 | 2.6 |
| SnEye | 4.7 | 3.9 | 4.2 | 4.3 | 3.8 | 3.8 | 3.5 | 4.0 | 4.0 | 4.4 |
| NarEye | 3.0 | 2.4 | 2.9 | 2.7 | 2.6 | 2.8 | 2.2 | 2.4 | 2.5 | 2.4 |
| Interorb | 4.1 | 3.2 | 3.7 | 3.9 | 3.1 | 3.7 | 3.5 | 3.6 | 3.9 | 2.8 |
| EarL | 1.6 | 1.2 | 1.2 | 1.3 | 0.9 | 1.5 | 1.3 | 1.1 | 1.5 | 1.5 |
| Internar | 1.5 | 1.6 | 1.5 | 1.6 | 1.2 | 1.4 | 1.4 | 1.4 | 1.4 | 1.3 |

Table 8. Mensural data for the types of Dierogekko poumensis, sp. nov. and D. inexpectatus, sp. nov. Abbreviations as in Materials and methods. All measurements in mm.

|  |  | -- |  | - - | - poumen | ensis |  | - |  | - i | expectatus |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\begin{aligned} & \text { MNHN } \\ & 2004.0021 \\ & \text { holotype } \end{aligned}$ | AMS R <br> 166977 <br> paratype | R AMS R <br> 166978 <br> e paratype | AMS R <br> 166979 <br> paratype | AMS R <br> 166980 <br> paratype | $\begin{aligned} & \text { CAS } \\ & 231839 \\ & \text { paratype } \end{aligned}$ | CAS <br> 231841 <br> paratype | CAS <br> 231850 <br> paratype | $\begin{gathered} \text { CAS } \\ 231851 \\ \text { paratype } \end{gathered}$ | $\begin{gathered} \text { CAS } \\ 231852 \\ \text { paratype } \end{gathered}$ | $\begin{aligned} & \text { MNHN } \\ & 2004.0025 \\ & \text { holotype } \end{aligned}$ |
| Sex | male | male | male | female | female | female | male | male | female | male | female |
| SVL | 34.3 | 35.0 | 36.2 | 35.6 | 34.7 | 35.7 | 38.3 | 34.6 | 34.6 | 36.5 | 39.5 |
| ForeaL | 4.4 | 4.1 | 4.4 | 4.5 | 4.7 | 4.3 | 4.7 | 4.7 | 4.8 | 4.4 | 4.9 |
| CrusL | 5.4 | 5.0 | 5.4 | 5.5 | 5.1 | 5.1 | 5.3 | 5.3 | 5.0 | 5.4 | 5.7 |
| TailL | 35.3 | 32.0 | 38.4 | 35.4 | 32.2 | 32.2 | 16.6 | 37.1 | 32.2 | 30.8 | 36.2 |
| (regen.) | 28.1 | 14.2 | 14.1 | 7.7 | 10.2 | 17.2 | broken | 10.3 | 5.7 | 20.3 | 25.8 |
| TailW | 5.2 | 4.8 | 4.5 | 5.0 | 5.0 | 5.0 | 5.1 | 5.2 | 5.0 | 4.8 | 4.8 |
| TrunkL | 14.0 | 13.5 | 13.2 | 13.4 | 13.6 | 14.2 | 16.9 | 14.5 | 13.7 | 14.9 | 17.4 |
| Headl | 10.5 | 11.3 | 10.9 | 9.7 | 10.7 | 9.1 | 10.7 | 9.4 | 10.2 | 9.7 | 10.5 |
| HeadW | 6.9 | 6.6 | 6.3 | 6.5 | 6.1 | 6.0 | 6.8 | 6.4 | 6.8 | 6.7 | 7.2 |
| HeadH | 4.4 | 4.4 | 4.4 | 3.9 | 4.2 | 3.4 | 3.9 | 4.4 | 3.6 | 4.4 | 4.1 |
| OrbD | 2.4 | 2.6 | 2.6 | 2.5 | 2.3 | 2.3 | 2.5 | 2.4 | 2.2 | 2.7 | 2.5 |
| EyeEar | 2.8 | 3.1 | 2.6 | 2.6 | 2.8 | 3.3 | 2.8 | 2.9 | 2.3 | 2.6 | 3.0 |
| SnEye | 3.7 | 3.5 | 4.0 | 3.5 | 3.3 | 3.6 | 3.4 | 3.7 | 3.3 | 3.5 | 4.6 |
| NarEye | 2.4 | 2.5 | 2.4 | 2.1 | 2.3 | 2.4 | 2.5 | 2.3 | 2.2 | 2.4 | 3.0 |
| Interorb | 3.2 | 3.1 | 3.1 | 3.2 | 2.9 | 2.9 | 3.4 | 3.4 | 3.1 | 2.8 | 3.5 |
| EarL | 1.2 | 0.9 | 1.0. | 1.0 | 1.0 | 1.0 | 1.1 | 1.4 | 1.1 | 1.1 | 1.4 |
| Internar | 1.2 | 1.1 | 1.1 | 1.4 | 1.1 | 1.2 | 1.1 | 1.2 | 1.3 | 1.5 | 1.3 |

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# Miconia amilcariana (Melastomataceae: Miconieae), a New Species from the Venezuelan Andes with Notes on the Distribution and Origin of Dioecy in the Melastomataceae 

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#### Abstract

Miconia amilcariana, known only from the Cordillera de Trujillo in the Venezuelan Andes, is described, illustrated, and compared with its presumed closest relatives in Miconia section Cremanium. This new species is distinguished by its 5 -merous unisexual flowers that are produced on different individuals (dioecy), 3-locular ovary, 5-7plinerved leaf blades, and indument on internodes, inflorescences, and abaxial foliar surfaces that consists of a mixture of stellate and asperous-headed hairs. A list of the known dioecious species of Miconia is provided together with comments on the geographical distribution and probable origin of dioecy in the Melastomataceae.


#### Abstract

Resumen Miconia amilcariana, conocida únicamente de la Cordillera de Trujillo en los Andes Venezolanos, es descrita, ilustrada, y comparada con sus presuntos parientes más cercanos en Miconia sección Cremanium. Esta nueva especie se distingue por sus flores unisexuales, 5 -meras, que se producen en individuos separados (dioecismo), ovario 3-locular, laminas foliares 5 -7-plinervadas, e indumento en los entrenudos, inflorescencias, y superficie foliar abaxial que consiste de una mezcla de tricomas estrellados y tricomas de cabeza áspera. Se incluye una lista de especies dioicas conocidas de Miconia con comentarios sobre la distribución geográfica y posible origin del dioecismo en las Melastomatáceas.


The late John J. Wurdack (1921-1998) identified many of the Melastomataceae collected during exploration of the flora of Guaramacal National Park (Portuguesa and Trujillo states) and neighboring areas in the Venezuelan Andes. In doing so he recognized the following as representing an undescribed species of Miconia Ruiz \& Pav., but for a variety of reasons he did not work up the available material for publication. We do so here with profound appreciation for the many contributions John made to our understanding of not only Melastomataceae, but also Venezuelan botany.

## Species description

## Miconia amilcariana Almeda \& Dorr, sp. nov.

Type.- Venezuela: Trujillo: Mpio. Boconó, El Campamento-Pele Ojo, bajando hacia Quebrada Honda, 1900-2120 m, 9-16 July 1998, B. Stergios 17582 (holotype, PORT!; isotypes, CAS!, US!). Figure 1.

Section Cremanium. Frutex vel arbor (1.5)2-10 m; ramuli primum obtuse sulcato-quadrangulati demum teretes sicut inflorescentia venae primariae et secundariae subtus pilis asperis et pilis stellati induti. Lamina $10.5-25 \times 4-12 \mathrm{~cm}$, elliptica vel oblongo-ovata vel ovata apice acuminata basi rotundata vel cordata, 5-7-plinervata, supra glabra. Panicula 6.5-12 cm multiflora; flores 5meri, bracteolis $0.5 \times 0.25 \mathrm{~mm}$ subulatis mox deciduis. Hypanthium (ad torum) 1 mm longum; calycis tubus non evolutus lobis interioribus $0.25 \times 0.25 \mathrm{~mm}$ dentibus exterioribus minutis ca. 0.3 mm eminentibus. Flores masculini: stamina isomorphica glabra; filamenta $1.5-1.6 \mathrm{~mm}$ longa; thecae $0.5 \times 0.5 \mathrm{~mm}$ obovato-oblongae late quadriporosae et 4-loculares; ovarium abortivum. Flores feminei: stamina abortiva, filamentis 0.5 mm longis, thecis ca. 0.4 mm longis; stigma peltatum; stylus $1-1.2 \times 0.2 \mathrm{~mm}$ glaber; ovarium 3-loculare et $3 / 4$ inferum, apice glabro.

Trees or understory shrubs (1.5)2-10 m tall with obtusely sulcate-quadrangular internodes that become terete with age. Uppermost cauline internodes, juvenile unexpanded leaves, and inflorescence rachis copiously but deciduously covered with a pale tan mixture of sessile-stellate and stalked-stellate and asperous-headed hairs. Leaves of a pair equal to subequal in size; petioles (1.7)2.5-7.5 cm long; blades $10.5-25 \times 4-12 \mathrm{~cm}$, elliptic, oblong-ovate to ovate, apex acuminate, base broadly rounded to nearly cordate, margin mostly entire but varying to crenate-serrulate or denticulate, 5-plinerved, the innermost pair of primary veins diverging from the median vein 2-10 mm above the blade base, adaxially $\pm$ glabrous at maturity, abaxially covered with a sparse to copious indument of sessile-stellate, stalked-stellate and asperous-headed hairs mostly on the primary and higher order veins with an inconspicuous scattering of minute orange-brown glands on the higher order veins and the actual blade surface. Inflorescence a terminal multiflowered panicle $6.5-12 \mathrm{~cm}$ long; bracteoles linear-subulate, 0.5 mm long and more or less 0.25 mm wide, glabrous, early deciduous and typically absent at anthesis. Flowers 5 -merous and unisexual on pedicels 0.5 mm long, covered with a scattering of rusty-brown glands. Hypanthia (at anthesis) 1 mm long to the torus, glabrous or with a few minute rusty-brown glands. Calyx tube obsolete, the calyx lobes $0.25 \times 0.25 \mathrm{~mm}$, glabrous, bluntly rounded-triangular, exterior teeth 5 , thickened and $\pm$ triangular or obconic, ca. 0.3 mm long but not projecting beyond the calyx lobes; torus glabrous on the abaxial side. Petals $1-1.1 \times 0.5-0.6 \mathrm{~mm}$, white, glabrous, obovate and $\pm$ concave, sometimes deeply notched or hooked apically in staminate flowers. Anthers white, isomorphic, cuneiform or obovoid, widest at the apex, 4 -celled and 4-pored, the filaments $1.5-1.6 \mathrm{~mm}$ long, anthers 0.5 mm long and ca. 0.5 mm wide apically in staminate flowers. the filaments ca. 0.5 mm long, non-polleniferous and collapsed anthers ca. 0.4 mm long in pistillate flowers; connective prolonged 0.25 mm below the thecae in staminate flowers but neither elevated nor appendaged. Ovary (in fruit) $3 / 4$-inferior, 3-locular, the apex glabrous. Style straight, glabrous, $1-1.2 \mathrm{~mm}$ long, stigma peltate in pistillate flowers, these structures vestigial and barely evident in staminate flowers. Berry $2-2.5 \times 2.5-3 \mathrm{~mm}$, globose, green flushed with pink when immature becoming bluish or purple-pink at maturity. Seeds $0.5-0.75 \mathrm{~mm}$ long, ovoid to ovoid-pyramidate, the testa irregularly granulate.

Distribution, Habitat and Phenology.- This species grows in openings created by roads and other clearings in lower montane and montane (cloud) forest in the Cordillera de Trujillo, the northeastern-most range of the Venezuelan Andes at $1,700-2,550 \mathrm{~m}$ (Fig. 2). Flowering and fruiting specimens have been collected in July and from September through January.

Paratypes.- Vexezlela: Lara: Mpio. Moran. Carretera desde Humacaro Alto hacia Guaito, 2,200 m. 14 Nov. 1984. van der Werff \& Rivero 7919. \& (US). Portuguesa: Mpio. Sucre, La Divisioria de la Concepción, $9^{\circ} 18^{\prime} \mathrm{N}, 70^{\circ} 06^{\prime} \mathrm{W}, 1.700 \mathrm{~m}, 23$ Oct. 1985. van der Werff et al. 7552, $0^{* 1}$ (PORT). Trujillo: Mpio. Boconó. Parque Nacional Guaramacal. vertiente norte ( $\left.9^{\circ} 14^{\prime} 59^{\prime \prime} \mathrm{N}, 70^{\circ} 12^{\prime} 43^{\prime \prime} \mathrm{W}\right), 2,100 \mathrm{~m}, 17-18$ Jun. 1995, Cuello et al. 999. (CAS. COL. MO. PORT. US). Ibid. ( $\left.9^{\circ} 14^{\prime} 48^{\prime \prime} \mathrm{N} .70^{\circ} 12^{\prime} 15^{\prime \prime} \mathrm{W}\right), 2,400 \mathrm{~m}, 1-3$ July 1995 , Cuello et al. 1077. $0^{\circ}$ (MO. PORT. US). Ibid. ( $9^{\circ} 14^{\prime} 38^{\prime \prime N} .70^{\circ} 13^{\prime} 12^{\prime \prime}$ W), $1.850 \mathrm{~m}, 15-16$ July 1995, Cuello et


Figure 1. Miconia amilcariana Almeda \& Dorr. A. habit; B. representative leaf (abaxial surface) with enlargement showing indument; C. staminate flower (longitudinal section) showing stamens and vestigial style; D. petal (staminate flower) showing notched apex; E. stamens from a staminate flower showing protruding septum; F. pistillate flower (longitudinal section) showing style, stigma, and vestigial stamens; G. petal (pistillate flower) showing rounded apex; H. vestigial stamen (pistillate flower); I. berry; J. seeds. (A, B, I and J from Stergios 19115; C-E from Tillett 739-614; F-H from Dorr \& Barnett 7529.)
al. 1185 (PORT); Parque Nacional Guaramacal, vertiente sur, ca. $9^{\circ} 12^{\prime} 45^{\prime \prime} \mathrm{N}, 70^{\circ} 09^{\prime} 51^{\prime \prime} \mathrm{W}, 2,300 \mathrm{~m}, 3-5 \mathrm{Jan}$. 1996, Cuello et al. 1327, 우 (CAS, K, PORT, US, VEN); Montañas de Misisi, carretera vieja Trujillo-Boconó (ca. $9^{\circ} 21^{\prime} \mathrm{N}, 70^{\circ} 18-19^{\prime} \mathrm{W}$ ), ca. 12 km by air NW of Boconó, 2,000-2,400 m, 31 Oct. 1990, Dorr \& Barnett 7529, ơ (NY, PORT, US), Ibid., 31 Oct. 1990, Dorr \& Barnett 7550, \& (NY, PORT, US, VEN), Ibid., 1 Nov. 1990, Dorr \& Barnett 7570, ㅇ (NY, PORT, US, VEN), Ibid., 1 Nov. 1990, Dorr \& Barnett 7572, of (NY, PORT, US, VEN); Parque Nacional Guaramacal, between Cerro El Diablo and Qda. Honda, ca. 11 km S of Boconó on road from Fundación La Salle to El Santuario ( $9^{\circ} 09^{\prime} \mathrm{N}, 70^{\circ} 17^{\prime} \mathrm{W}$ ), ca. 2,100 m, 21 July 1995, Dorr et al. 8219, ơ (CAS, PORT, US); Parque Nacional Guaramacal, trail from la Laguna de las Aguas Negras to la Qda. Salvaje, N slope, $9^{\circ} 19^{\prime}$ N, $70^{\circ} 11^{\prime} \mathrm{W}, 27$ Oct. 1998 , Dorr et al. 8281 , \& (AAU, CAS, PORT, US); Parque Nacional Guaramacal, road from Boconó to Guaramacal, SE of Boconó, ca. 15 km from the post of the park guards, S slope, $9^{\circ} 13^{\prime} \mathrm{N}, 70^{\circ} 12^{\prime} \mathrm{W}, 2$ Nov. 1998, Dorr et al. 8416 (CAS- $\sigma^{\circ}$, CTES- 9 , F- $\uparrow$, NY- 9 , PORT, USㅇ) ; Parque Nacional Guaramacal, sector vertiente norte, carretera al Páramo Guaramacal, 2,100-2,550 m, Jan. 2000, Stergios 19115 (PORT, US), Ibid., Stergios 19123, ㅇ (PORT, US); Parque Nacional Guaramacal, sector quebrada Honda-Pele Ojo, El Santuario, 1,950-2,100 m, Jan. 2001, Stergios \& Caracas 18986, of (CAS, PORT, US- $甲$ ); Parque Nacional Guaramacal, vertiente norte, camino Laguna de los Cedros-cresta del páramo, $9^{\circ} 07^{\prime} \mathrm{N}, 70^{\circ} 16^{\prime} \mathrm{W}$, Jan. 1991, Stergios \& Palacios 18690, ㅇ (PORT, US); Cerro Guaramacal, Boconó, bajando hacia el caserío de Guaramacal, 25-26 Nov. 1982, Stergios et al. 4746, ơ (PORT, US); Parque Nacional Guaramacal, sector quebrada Honda de El Santuario, 1,880-2,000 m (UTM: 1012298N, 359185E), Nov. 2001, Stergios et al. 19365 , bud (PORT, US); 4-5 km along old Boconó-Trujillo road, from crossroad with new highway at 2 km S of lateral to Burbusay, ca. 2,400 m, 6 Sep. 1973, Tillett 739-614, $0^{7}$ (US).

DISCUSSION. - Based on its obovoid-oblong anthers with a wide 4-pored apex and protruding septum, Miconia amilcariana is assigned to section Cremanium (D. Don) Naudin, the largest (with some 214 species) of the 10 currently recognized sections of Miconia. The distinctive features of M. amilcariana include its 5-merous unisexual flowers that are produced on different individuals (dioecy), anther pores that are essentially truncate or slightly inclined ventrally at the apex, peltate stigma on pistillate flowers, 3-locular ovary, 5-7-plinerved leaf blades, and indument on internodes and abaxial foliar surfaces that consists of a mixture of sessile- and stalked-stellate hairs, and asper-ous-headed hairs.

Among the species of section Cremanium, Miconia amilcariana is most similar to M. laetevirens L. Uribe of Colombia and M. tabayensis Wurdack of Venezuela. The former differs from the new species in having hermaphroditic flowers, 3-nerved or shortly 3-plinerved leaf blades, elliptic to obovate-spatulate bracteoles that are persistent, and a clavate-truncate to subcapitate stigma. The anthers of both $M$. laetevirens and $M$. amilcariana are similar in shape and in being 4-loculed and 4-pored but the former differs in having the two dorsal anther sacs positioned above (superposed) the two ventral anther sacs with all the apical pores conspicuously inclined ventrally to give the overall anther a somewhat curved aspect (see Uribe Uribe 1966). In M. amilcariana all the locules of each anther diverge from the same basal position to give the anther a straight posture.

In overall morphological similarities, Miconia amilcariana appears to be most closely related to M. tabayensis, another dioecious species (Wurdack 1973). The latter has leaf apices that are shortly obtuse-acuminate (vs. acuminate to long-acuminate), leaf bases that are obtuse to rounded (vs. broadly rounded to nearly cordate), and linear-oblong bracteoles that are $0.7-1 \mathrm{~mm}$ long (vs. linear-subulate bracteoles that are 0.5 mm long). The most striking feature of $M$. tabeyensis that readily distinguishes it from $M$. amilcariana is the indument on branchlet internodes, the inflorescence, and abaxial foliar surfaces. This indument, which is fairly dense and persistent, consists of inconspicuously septate simple hairs $0.5-1.2 \mathrm{~mm}$ long that are somewhat crisped and often forked or barbed distally. In $M$. amilcariana, the indument which can be sparse to copious but tardily deciduous consists of a mixture of sessile- and stalked-stellate hairs intermixed with asperous-headed hairs, all of which are prevailingly less than 0.5 mm in length. Each species also appears to occur in a different region of montane Venezuela. Miconia amilcariana is known from several collections
made in the northeastern-most range of the Venezuelan Andes at $1,700-2,550 \mathrm{~m}$. Miconia tabayensis, also endemic to the Venezuelan Andes, has been collected only a few times above Mérida and in a region of the Cordillera de Mérida further south and west near Pueblo El Cobre at 2,300-2,800 m.

The unisexual flowers of Miconia amilcariana consistently have vestigial organs of the other sex (Fig. 1F and 1 H ; Fig. 1C). This is common for dioecious species in families that are largely hermaphroditic like the Melastomataceae. Nectar is typically the attractant in female flowers of dioecious species (Proctor et al. 1996) but sterile anthers may be the prime attractant in female flowers where pollen is the prime reward. This is likely the case in small-flowered species like Miconia section Cremanium that are probably visit-


Figure 2. Distribution of Miconia amilcariana Almeda \& Dorr in the Venezuelan Andes; the darker line more or less defining these mountains. ed by generalist pollinators.

Although bisexual (hermaphroditic) flowers are the predominant form of sex expression in the angiosperms, dioecy occurs in a wide range of flowering plant families (Endress 1994; Grant 1975; Yampolsky and Yampolsky 1922). According to recent estimates, dioecy occurs in about 7-10\% of the world's flora (Allem 2004; Proctor et al. 1996). It is common in isolated insular floras, shrubs of the Mediterranean region, and in nearly $25 \%$ of rain forest trees (Proctor et al. 1996). Generalizations on the advantages of dioecy continue to be debated (Allem 2004) since each species or group of species has undoubtedly responded to different selective pressures (Bawa, 1980; Proctor et al., 1996). The long-held hypothesis that the evolution of dioecy has led to the optimization of outbreeding is increasingly questioned since the evidence for an association between dioecy and agamospermy is mounting (Allem 2004). Agamospermy is known or suspected in hermaphroditic species of Miconia and related genera (Almeda 2003; Almeda and Chuang 1992; Goldenberg and Shepherd 1998; Renner 1989) but, as yet, we have no definitive information about reproductive biology of the dioecious species of Miconia, many of which are still little-collected and poorly known.

Among the approximately 172 genera of Melastomataceae, true dioecism is known only in Miconia, a neotropical genus with over 1,050 recognized species. According to our preliminary list (see Appendix I) there are 37 dioecious species of Miconia (including 42 taxa). Thirty-two of these taxa occur only in the Andes of South America and 23 of them are restricted to or have geographic ranges including Peru. Additionally, all of the dioecious species are in section Cremanium except M. stenophylla, which has recently been placed in section Chaenopleura (DC.) Triana by Wurdack (1980). Sections Cremanium and Chaenopleura have obovate or cuneate anthers but the former has apical pores and the latter dehisces by slits. Both sections are closely related and species placed in the latter have been transferred to the former because the distinctions in stamen morphology are not always clear. In a recent molecular phylogeny of the Miconieae ( Michelangeli et al. 2004) the few sampled species in these two sections form a clade which suggests that dioecy in Miconia may have
arisen only once. If this is born out by more comprehensive sampling, it also seems possible that dioecy in Miconia originated in the South American Andes.

Etymology.- This species is named for Amilcar Bencomo, Superintendent of Guaramacal National Park. With few tangible resources at his disposal, he has been fiercely protective of the park, an important refuge for Andean flora and fauna and an essential watershed for the people of Barinas, Portuguesa, and Trujillo states. Additionally, he has been an outstanding friend of science and has enthusiastically supported projects that contribute to expanding our knowledge of the natural history of Guaramacal.

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## Literature Cited

Allem, A.C. 2004. Optimization theory in plant evolution: An overview of long-term evolutionary prospects in the angiosperms. The Botanical Review 69:225-251
Almeda, F. 2003. Chromosome cytology and taxonomy of the red goblet-flowered species of Clidemia (Melastomataceae: Miconieae) in Central and South America. Novon 13:161-169.
Almeda, F., and T.I. Chlang. 1992. Chromosome numbers and their systematic significance in some Mexican Melastomataceae. Systematic Botany 17:583-593.
Bawa, K.S. 1980. Evolution of dioecy in flowering plants. Annual Review of Ecology and Systematics 11:1539.

Endress, P.K. 1994. Diversity and Evolutionary Biology of Tropical Flowers. Cambridge University Press, Cambridge, England, UK. 511 pp.
Goldenberg, R., and G.J. Shepherd. 1998. Studies on the reproductive biology of Melastomataceae in "cerrado" vegetation. Plant Systematics and Evolution 211:13-29.
Grant, V. 1975. Genetics of Flowering Plants. Columbia University Press, New York, New York, USA. 514 pp.
Michelangeli, F., D.S. Penneys, J. Giza. D. Soltis, M.H. Hils a.id J.D. Skean, Jr. 2004. A preliminary phylogeny of the tribe Miconieae (Melastomataceae) based on nrITS sequence data and its implications on inflorescence position. Taxon 53:279-290.
Proctor. M., P. Yeo, and A. Lack. 1996. The Natural History of Pollination. Timber Press, Portland, Oregon, USA. 479 pp .
Renner. S. S. 1989. A survey of reproductive biology in neotropical Melastomataceae and Memecylaceae. Annals of the Missouri Botanical Garden 76:496-518.
Uribe Uribe, L. 1966. Sertula Florae Colombiae, X. Nuevas especies de Miconia (Melastomataceae). Caldasia 9(45):457-465.
Wurdack, J.J. 1967. Plants collected in Ecuador by W. H. Camp - Melastomataceae. Memoirs of the New York Botanical Garden 16:1-45.
Wurdack, J.J. 1973. Melastomataceae. In T. Lasser, ed., Flora de Venezuela 8(1\&2):1-819.
Wurdack. J.J. 1980. Melastomataceae. In G. Harling and B. Sparre. eds.. Flora of Ecuador 13:1-406.
Yampolsky, C., and H. Yampolsky. 1922. Distribution of sex forms in the phanerogamic flora. Bibliotheca Genetica 3:1-62.

## Appendix I

## The Known Dioecious Taxa of Miconia and Their Geographic Distributions

All of these species are placed in section Cremanium except M. stenophylla which was originally placed in section Cremanium but subsequently assigned to section Chaenopleura by Wurdack (1980).
M. amilcariana Almeda \& Dorr - Venezuela
M. aprica Gleason - Peru
M. boliviensis Cogn. - Bolivia
M. bracteolata (Bonpl.) DC. - Colombia, Ecuador, Peru \{perhaps dioecious, in part, according to Wurdack (1967, 1980) \}
M. brevistylis Cogn. - Peru
M. caerulea (D. Don) Naudin ssp. caerulea - Peru
M. caerulea (D. Don) Naudin ssp. vilcabambae Wurdack - Peru
M. choriophylla Wurdack var. choriophylla - Peru
M. choriophylla Wurdack var. brevifolia Wurdack-- Peru
M. clathrantha Triana ex Cogn. - Ecuador, Peru
M. coelestis (D. Don) Naudin - Bolivia, Peru
M. coriacea (Sw.) DC. - Costa Rica, Dominica, Guadeloupe
M. cyanocarpa Naudin var. cyanocarpa - Bolivia, Peru
M. dasyclada Wurdack - Peru
M. dielsii Markgr. - Ecuador, Peru
M. dioica Wurdack - Venezuela
M. divergens Triana - Colombia, Ecuador (poorly known, but probably dioecious as implied by Wurdack, 1980)
M. elongata Cogn. - Bolivia, Peru
M. galactantha Naudin - Peru, Bolivia
M. glaberrima (Schltdl.) Naudin - Belize, Guatemala, Honduras, Mexico
M. globuliflora (Rich.) Cogn. var. globuliflora - Martinique, Montserrat, Nevis, St. Lucia
M. globuliflcra (Rich.) Cogn. var. dominicae R.A. Howard \& E.A. Kellogg - Dominica, Montserrat, St. Kitts (incl. Nevis)
M. globuliflora (Rich.) Cogn. var. vulcanica (Naudin) R.A. Howard \& E.A. Kellogg — Guadeloupe
M. hemenostigma Naudin - Guatemala, Mexico
M. micropetala Cogn. - Bolivia, Ecuador, Peru
M. minuta Gleason - Colombia, Ecuador
M. oligotricha (DC.) Naudin - Mexico
M. paradisica Wurdack - Peru
M. peruviana Cogn. - Peru
M. polychaeta Wurdack - Peru
M. polygama Cogn. - Bolivia
M. pulverulenta Ruiz \& Pav. - Peru
M. purulensis Donn. Sm. - Guatemala, Honduras, Mexico
M. reburrosa Wurdack - Ecuador
M. rubens (Sw.) Naudin - Colombia, Jamaica, Venezuela
M. stenophylla Wurdack - Ecuador, Peru
M. sterilis Gleason - El Salvador
M. tabayensis Wurdack - Venezuela
M. thaminantha Wurdack ssp. thaminantha - Peru
M. thaminantha Wurdack ssp. huanucensis Wurdack - Peru
M. valida Cogn. - Bolivia
M. vitiflora J. F. Macbr. - Peru

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# A New Species of Typhlacontias (Reptilia: Scincidae: Feylininae) from Western Tanzania 

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#### Abstract

A new species of Typhlacontias is described from the Katavi National Park in western Tanzania, extending the range of the genus 800 km to the northeast from the nearest locality for T. gracilis in western Zambia. It differs from the latter species in two head shield fusions.


The genus Typhlacontias Bocage was revised by Haacke (1997). He recognised six species, four from the northern Namib Desert and two, T. gracilis and T. rohani, from the Kalahari sand regions of southeastern Angola, northwestern Namibia, northern Botswana, western Zimbabwe (the latter recently recorded from south of Bulawayo [Broadley and Wilson 2005]) and southwestern Zambia (Fig. 1). It was therefore quite unexpected when a population belonging to the latter complex was found in the Katavi National Park in western Tanzania, 800 km northeast of Kabompo, the nearest locality for T. gracilis, which it closely resembles. This taxon is described below.

A recent study of the phylogeny of the Scincidae of sub-Saharan Africa, based on molecular data, indicates that the genus Typhlacontias is sister to a clade including Feylinia and Melanoseps, so these genera are now assigned to the subfamily Feylininae (Whiting et al. 2003).


Figure 1. Distribution of the Typhlacontias gracilis complex in central Africa.

## Material and Methods

Meristic data from Haacke (1997) were augmented by additional data from Zambian material of $T$. gracilis in the Natural History Museum of Zimbabwe (NMZB) and the arrangement of head shields in the new taxon was compared with them.

Scale counts (ventrals and subcaudals) were made using a Watson M8 binocular microscope. Head shield terminology follows Haacke (1997). Snout-vent and tail measurements were made using a white-face tape, but are not precise, as the very fragile tail in these animals makes this operation difficult.

## Systematics

## Typhlacontias kataviensis Broadley, sp. nov.

Figures 2-3.
Holotype.- California Academy of Sciences (CAS) 227747 (field number 03660). An adult from Mswala Sands, bordering the Katavi floodplain [ $06^{\circ} 38^{\prime} 33^{\prime \prime} \mathrm{S} 31^{\circ} 12^{\prime} 32^{\prime \prime} \mathrm{E}$ ] at ca. 850 m in the Katavi National Park, western Tanzania. Collected by T.A. Gardner on 6 March 2003.

Paratypes. - CAS 227745-227746, 227748 with the same data as the holotype. CAS 227740 from Katisunga Mbuga [ $06^{\circ} 52^{\prime} 43^{\prime \prime} \mathrm{S} 31^{\circ} 11^{\prime} 04^{\prime \prime} \mathrm{E}, 13$ April 2003] and CAS 227749, 14 April 2003 and 231982 (no date) from Jaribu Mtgao [ $06^{\circ} 54^{\prime} 03^{\prime \prime} \mathrm{S} 31^{\circ} 12^{\prime} 21^{\prime \prime} \mathrm{E}$ ], both these localities being on sand ridges bordering the Katisunga floodplain, Katavi National Park. Collected by pitfall trapping and superficial manual digging.

Etymology.- This species is named for the Katavi National Park, to which it may prove to be endemic.

Diagnosis. - Close to T. gracilis, but usually distinguished by the fusion of the 'third supraocular' (Haacke 1997) with the upper anterior temporal (an aberration in the type of T. gracilis Haacke 1997) and the frontoparietal with the upper second temporal (Fig. 2). The ventral counts average slightly higher than those for either T. gracilis or T. rohani, while the subcaudal counts average higher than those of T. gracilis, but are lower than those of T. rohani (Table 1).

Description.- Large rostral not strongly notched laterally. Dorsal head shields typical for the genus, with frontonasal slightly wider than internasal and frontal. A prefrontal wedged between frontonasal and two supraoculars; the 'third supraocular' usually present in T. gracilis is fused with the upper anterior temporal and contacts the frontal, while the frontoparietal of T. gracilis is fused with the upper second tem-


Figure 2. Typhlacontias kataviensis: lateral view of the head of the holotype (CAS 227747). KEY: cs $=$ chin shield; f $=$ frontal: $\mathrm{fn}=$ frontonasal; in = internasal; $\mathrm{ip}=$ interparietal; $11=$ lower labial; $\mathrm{lo}=$ loreal $; \mathrm{m}=$ mental $; \mathrm{p}=$ parietal $; \mathrm{pf}=$ prefrontal; $\mathrm{r}=$ rostral; so $=$ supraocular; $\mathrm{t}=$ temporal; $\mathrm{ul}=$ upper labial; $\mathrm{x}=$ 'supraocular 3' + upper anterior temporal; y $=$ frontoparietal + upper second temporal. poral; there is a single lower preocular and two postoculars (Fig. 2). There are six upper labials, the third entering the orbit, and four lower labials. Midbody scale rows 18 , ventrals 137 , subcaudals 72 .

Table 1. The Typhlacontias gracilis complex. Variation in size, body proportions and scale counts. (partly after Haacke 1997)

| Species | $n$ | $\begin{aligned} & \text { Max } \\ & \text { SVL } \end{aligned}$ | \% Tail/SVL |  |  | Ventrals |  |  | Subcaudals |  |  | Vertebrae |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | Range | Mean(n) | SD | Range | Mean(n) | SD | Range | Mean(n) | SD |  |
| T. gracilis | 195 | 86 | 38-61 | 48.65(55) | 4.66 | 121-147 | 33.55(134) | 4.83 | 56-68 | 62.05(56) | 3.25 | 68 |
| T. kataviensis | 7 | 76 | 49-58 | 54.66(3) | 4.93 | 132-141 | 136.86(7) | 3.18 | 56-72 | 66.0 (3) | 8.72 |  |
| T. rohani | 233 | 90 | 48-73 | 57.0(69) | 5.98 | 124-146 | 134.3(193) | 4.57 | 64-84 | 69.4(73) | 11.3 | 62,63,66 |

Scale counts for the paratypes are summarised in Table 1. In CAS 227745 the frontoparietal is not fused with the upper second temporal.

Colouration.-Buff, a blackish blotch on the head, the paravertebral rows dark-centred, forming ragged blackish lines from nape to tip of original tail, lateral scale rows also dark-centred (Fig. 3). This pattern is remarkably similar to that of the fossorial skink Ophiomorus brevipes of Iran (Anderson and Leviton 1966).


Figure 3. Typhlacontias kataviensis: paratype CAS 231982 from Jaribu Mtgao, Katavi National Park. Note the lack of stripes on the regenerated portion of the tail. Photo by T.A. Gardner.

Size.- Holotype 113 (72 + 41) mm, but CAS 227745 and 227749 both measure 76 mm in snout-vent length (tails truncated or regenerated).

Distribution.- Only known from sand ridges bordering flood plains in the Katavi National Park in western Tanzania.

Other material examined.- Typhlacontias gracilis: Zambia: Kabompo Boma (1324C1) NMZB 501, 2822, 3405-6, 4967; Kalabo (1422D3) NMZB-UM 4811-4, 6768, 6770-9, 6781, 6783-5, 6789-90, $6792,6794,6796-9,7870-99,10049,10051,10055-60,21032,21034-42,21044-50,21052-7,21059-60$, 21062-8, 21070-96, 21098-21103, 21105-16, 21118-43, 21145-8, 21150; Lealui (1523A1) MNHN 20.89-95 (type series); 8 km NE of Mongu (1523A1) NMZB 15983-4; Ndau School (1522B4) NMZB 15986-8, 16023-6, 16044.

## Discussion

This new population of Typhlacontias lies ca. 800 km northeast of the nearest known T. gracilis in Zambia, with other populations inhabiting the Barotse floodplain bordering the upper Zambezi. However, the missing lectotype of Melanoseps longicauda Tornier 1900, ZMB 16900 from 'Massai Steppe', matches a Typhlacontias in proportions, scale counts and especially colour pattern, and if eventually found, it could prove to represent another Typhlacontias population much further to the northeast, but still on the track of the transient 'arid corridor' linking the southwest arid region with the Horn of Africa.

## Acknowledgments

I am grateful to Toby Gardner for collecting the type series of Typhlacontias kataviensis and Robert Drewes for sending this material to me for study and for facilitating the publication of this paper. Sheila Broadley did the ventral and subcaudal scale counts on the type series and a large sample of T. gracilis.

## Literature Cited

Anderson, S.C., and A.E. Leviton. 1966. A review of the genus Ophiomorus (Sauria: Scincidae), with descriptions of three new forms. Proceedings of the California Academy of Sciences, ser. 4, 33:499-534.
Broadley, D.G., and V.J. Wilson. 2005. Geographical distribution: Reptilia; Sauria; Scincidae Typhlacontias rohani Angel. African Herpetological News 38:31.
Haacke, W.D. 1997. Systematics and biogeography of the southern African scincine genus Typhlacontias (Reptilia: Scincidae). Bonner zoologische Beiträge 47:139-163.
Whiting, A.S., A.M. Bauer, and J.W. Sites, Jr. 2003. Phylogenetic relationships and limb loss in sub-Saharan African scincine lizards (Squamata: Scincidae). Molecular Phylogenetics and Evolution 29:582-598.

# Some Thoughts on the Development of a Diatom Flora for Freshwater Ecosystems in the Continental United States and a Listing of Recent Taxa Described from U.S. Freshwaters 

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Although there has been over one hundred and fifty years of work (Ehrenberg 1854; Bailey 1851), we are far from an understanding of the freshwater, recent diatom flora of the United States. Previous efforts to catalogue the taxa occurring in the surface waters include a listing of approximately 525 taxa by Boyer ( $1927 \mathrm{a}, \mathrm{b}$ ) and illustrations of nearly 500 freshwater (and marine) taxa by Wolle (1890). The most widely utilized flora, produced by Patrick and Reimer $(1966,1975)$, included well over 800 taxa, but was incomplete on several levels. It included only araphid and naviculoid forms, dealt with taxa reported up to 1960, and was not exhaustive in its treatment of forms reported up to that time. Regional floras and summaries include the Laurentian Great Lakes by Stoermer and Kreis (1978) and Stoermer et al. (2000) (with over 2100 entries), Ohio (Collins and Kalinsky 1977, approximately 900 taxa), Montana (Prescott and Dillard 1979, with over 540 taxa), Kentucky (Camburn 1982, with just over 500 taxa), Illinois (Dodd 1987, with about 425 taxa), and Nebraska (Elmore 1922, with 234 taxa). Summaries from river systems include the work of Hohn and Hellerman (1963, who enumerated just over 475 taxa) and Patrick (1961, with 280 taxa), while Camburn et al. (1984-1986) and Camburn and Charles (2000) documented over 450 taxa from acid lakes in the eastern U.S. There are a large number of individual floristic works for individual systems or specific areas, such as Rushforth and Squires (1985) who reported $2 . \ldots$. ....n taxa from Utah Lake and Kingston et al. (1983) who found 425 taxa from Grand Traverse Bay, Lake Michigan. Because many of these reports for individual localities were generated by ecologists who did not have a taxonomic perspective, it could be argued that the numbers of taxa would actually be more than those detailed in these reports.

Recently, discussions in a number of forums, including Diatom-L, have called for a comprehensive flora of Recent freshwater diatoms of the United States. This call has been especially strong from ecologists, many of whom are engaged in national, state, or local water quality monitoring programs that specify diatoms be used in estimating water quality. These programs are not currently supported by a comprehensive English-language flora (let alone one based on the flora of the country), and the disparate (and growing) literature in the field is becoming inaccessible to many of these workers. The call by ecologists for a flora in support of their work is refreshing, since a large number of previous and current studies lacked such a basic, but important tool. This goes back to major studies on U.S. rivers undertaken in the late 1950s through the early 1970s, (Williams and Scott 1962) as well as programs focused on lakes, for example the U.S. Environmental Protection Agency's country wide survey of lake phytoplankton in the 1970s (U.S. EPA 1975) and the EMAP program initiated in 1980s (e.g., Paulsen and Linthurst 1994; Dixit and Smol 1994) and the current U.S. Geological Survey's NAWQA program focused on rivers (Porter et al. 1993). Not only have these projects been carried out without a flora, but until the publication on the freshwater algae of

North America (Wehr and Sheath 2003), even the most recent key to genera in English dated from the late 1950s to the early 1980s (Patrick 1959; Vinyard 1979; Barber and Haworth 1981) and reflected the taxonomic approach of those times.

A flora, of course, not only supports applied research projects such as water quality monitoring, but a wide range of basic research questions are implicit in and supported by a flora, including taxonomic revisions and monographs, phylogeny reconstruction, biogeographic studies, as well as ecological, physiological, restoration and conservation biology research programs (Kociolek and Stoermer 2001). The linkage between the floras of central Europe (Krammer and Lange-Bertalot 1986, 1988, 1991a, b) and New Caledonia (Moser et al. 1998) and revisions of the genera Cymbella (Krammer1997a, b, 2003), Pinnularia (Krammer 1992, 2000), Navicula (Lange-Bertalot 2001), Gomphonema (Reichardt 1995, 1999; Reichardt and Lange-Bertalot 1991), Brachysira, and Nupela (Lange-Bertalot and Moser 1994) is clear.

## The Challenge of a Flora for the United States

Lack of a flora for the United States is probably due less to the tremendous flux in taxonomy, proliferation of taxonomic literature, or the fact that we are still in a discovery phase for the description of diatoms (Fourtanier and Kociolek 1999), but, rather, a number of other basic, practical considerations. These considerations include:

Size of the country: The continental United States is approximately 9.8 million square kilometers, with the 48 contiguous states stretching a distance equivalent West to East from Portugal to the Ukraine, and North to South from the United Kingdom to North Africa (2005, Times Atlas of the World).

Diversity of habitats: Habitats range from subtropical to boreal, three marine coasts to numerous, substantial mountain ranges and major river systems of the Mississippi, Missouri, Columbia, Colorado and Potamac rivers. Potapova and Charles (2003) have discussed the variables effecting the distribution of riverine diatoms across the U.S., and noted that environment, geography and altitude factors help account for the biogeographic distributions of diatoms. Because many of the evaluations have been generated by goal-oriented ecological studies, many times diverse habitats have not been sampled. An example of such an ecosystem might be deep-living communities in lakes (Stoermer 1981).

Still relatively unexplored: The size and diversity of habitats have contributed to the situation in that the country is relatively unexplored from a phycological perspective, and from the perspective of a diatomist. In addition to the 3 attempts to synthesize knowledge about the diatom flora of the United States (Boyer 1927a, b; Wolle 1890; Patrick and Reimer 1966, 1975), there have been regional floras and summaries (Kociolek and Spaulding 2003; see above). While the physical sample resources are probably already in place to undertake a flora (housed primarily at the Academy of Natural Sciences of Philadelphia, California Academy of Sciences, and the Botany Department of the Smithsonian Institution), most have not been "explored" to any great degree. There are still relatively few samples, however, from major parts of the country (see below).

Number of people to do the work: The number of formally trained freshwater diatom taxonomists in the United States is modest, relative to the size of the country. Though training programs at universities have existed for an extended period, both in terms of specialized summer courses and short-term training sessions as well as Master's and Doctoral. programs, there are probably fewer of these today than even when I began my career in the early 1980s. In fact, we have seen only a single generation of expertise become resident at an institution; continuity has been lost after the founding professor/lab has been dismantled. A lack of continuity and sustainability of tax-
onomists and curators in universities and museums can also be argued, as long-term commitment has been replaced by short-term projects. Short-term projects may result in the deposition of slides into collections; however, systematic treatments and description of taxa new to science are rare or lacking. Overall. the intellectual infrastructure is diminishing, as the focus in many institutions of higher learning tends towards a more reductionist perspective. Kociolek and Stoermer (2001) discuss this issue and the continuing need to include a broader community of taxonomists, many trained outside the U.S. university system, to apply expertise in the identification of diatoms. This expertise will have to include people whose main interest has not been taxonomy, but who use taxonomy to help answer questions related to ecology, climatology and geology.

## Tools to Carry Out a Modern Flora

A modern flora is both a synthesis of existing data and discovery of new information, whether it results in descriptions of new species, new records, and/or new information on the distribution (expanded or more narrowly circumscribed than previously thought) of taxa. A basic approach is to understand first what has been reported previously, and confirm (or refute) the presence those taxa. Such a synthesis requires some basic tools. These tools include:

Checklist: This is a complete listing of taxa reported from an area (in the context of this discussion, the 48 contiguous United States). Such a checklist does not currently exist. Stoermer and Kreis (1978) and Stoermer et al. (2002) have generated such a list for the Laurentian Great Lakes, and as indicated above, such lists have been generated for a few parts of the country. An effort is now underway to compile this list, reviewing the hundreds of reports of diatoms from the published literature. The list currently contains over 4500 names. This is not "THE Final Definitive" list of taxa, however; it will be reduced and also receive additions as it is applied in floristic research. This list, for example, contains synonyms of two sorts. The first kind of synonym in such a list will be names based on a single type (a nomenclatural synonym). For example, Achnanthes lanceolata (Brébisson) Grunow and Planothidium lanceolatum (Brébisson) Round \& Bukht. would both be included in such a list, but the two names refer to a single entity, based on a type initially described by Brébisson. The second kind of synonym that would occur in a checklist of this kind is one where two (or more) taxa described from different types are considered a single entity (a taxonomic synonym). An example of this sort would be whether Cymbella diluviana (Krasske) Florin and C. couleensis Sovereign are the same (Patrick and Reimer 1975) or different (Sovereign 1963) species. Evaluation of these situations can be resolved by monographic or revisionary studies. The initial list of $4400+$ names based on the published literature will certainly be reduced, due to synonymy, but also greatly expanded by additions.

Nomenclature: One way to track the nomenclatural synonymies is with a database of names. The California Academy of Sciences is undertaking this mammoth effort and has developed a database of over 55,000 entries. The database includes the names included in all of the previously published catalogues (Habirshaw 1877; Chase 1885, 1907; Peragallo 1897-1903; Mills 1933-1935; Van Landingham 1967-1979), entries from two institutional card files (New Species File from ANSP and the Index Nominum Algarum, University of California, Berkeley) and additional entries from the primary literature. Discrepancies with respect to the information from these sources are tracked in the database (name, author, place, date and specifics of publication) and are being rectified by reviewing the original publications. This database has been demonstrated at a number of national (North American Diatom Symposium) and international (International Diatom Symposium) meetings. Publication of this work is expected to commence in 2006; it is expected ultimately to consist of 4-6 volumes.

ACCESS TO TYPES: For comparison and verification of taxon identities, it is preferable in floristic work to be able to access the type(s) of the taxa under consideration. This was the approach taken by Patrick and Reimer in their floristic work, and it continues to provide great added value to that work and subsequent works. Several publications can facilitate identifying the location of types of diatom taxa from freshwater environments, including those of Mahoney and Reimer (1997), Kociolek et al. (1999), Lange-Bertalot et al. (1996 on the collection of Krasske), Krammer (Cymbella 1997a, b, 2002; Pinnularia 1992, 2000), Williams (Diatoma 1985) and the excellent work by Simonsen (1987) on the collection of Friedrich Hustedt. From the preliminary list of $4400+$ names in the checklist being developed, about $50 \%$ of the names are associated with types that can be traced to a specific institution and material (sample and/or slide). When the names attributed to Agardh, Bailey, Cholnoky, Ehrenberg, Gregory, Grunow, Kützing, Rabenhorst, W. Smith, and Van Heurck are included (since we know the institutions those collections are housed, though specific samples may not have been identified as the types for each taxon), the percentage of types accessible rises to nearly $85 \%$. This suggests access to types for comparison could be accomplished for many of the names on the checklist and this critical tool could be in place to support a flora project. In fact, development of a research tool that indicates the range of morphological expression of the types would be one of the first steps in undertaking the flora for the U.S.

Samples: Access to samples for floristic work is important for a number of reasons. Verification of taxa reported in the literature many times requires access to material, that is the samples or slides used by the author who described the flora. Extant samples also allow those involved in the production of the flora to assess the areas under study that require additional sampling. Many workers in the U.S. have excelled in ensuring their collections are accessible in some fashion. A tragedy has been that the samples from several major national water quality monitoring/estimation efforts were not retained, thereby negating any way to leverage those samples for future research, including development of a flora, later comparative work, etc. The role museums play in storing, caring for and making accessible these important scientific research resources is hugely important. Collections of Patrick, Reimer, Boyer, Theriot, and many types of freshwater diatoms described from the United States and elsewhere are housed at ANSP, while the collections of Kociolek, Stoermer, Van Landingham, Elmore, Rushforth, Sovereign and G.W. Prescott are housed at CAS. Nearly $90 \%$ of the types for which we can identify a slide are housed at either ANSP or CAS (Table 1). Samples from the NAWQA project are housed at both institutions. The Botany Department of the Smithsonian Institution houses about 15,000 slides from one of EPA's water quality monitoring projects. It includes most of the major river systems in the continental U.S., which were sampled monthly over a period of time. In some cases the period of sampling was only for 2 years, but others the sampling period was continuous for a decade or more. While the collection resources currently available are impressive, and could support in large part an effort to document the freshwater diatom flora of the United States, it seems clear that some parts of the country are not well represented in these collections. These areas include, but are not limited to, the Rocky Mountains, the Sierra Nevada Mountains, the Deep South, southern Plains states, southern California, and the southwestern U.S.

## Preliminary List of Diatoms Described from U.S. Freshwaters

One approach to establishing the flora of the U.S. would be to document those taxa that have been described as new from U.S. localities; a preliminary list of these taxa is presented in Table 1.

Nearly 600 taxa have been described as new from freshwater environments in the continental United States. Genera with the most taxa described from the U.S. include Navicula (148 taxa),

Pinnularia (66 taxa), Gomphonema (39 taxa), Cymbella (31 taxa), and Eunotia (31 taxa), Nitzschia (27 taxa), Achnanthes (24 taxa) and Neidium (23 taxa). There are several genera in which a single taxon has been described, including Adlafia, Diploneis, Tetracyclus, Cymatopleura, Cyclostephanos, Mastogloia, Peronia, and Pleurosigma; many of these genera are better represented in the brackish or marine environments, or part of relatively small genera.

It is somewhat surprising that the genera Cyclotella and Stephanodiscus have so few new taxa described from the U.S. Likewise, the number of species described from U.S. in the nitzschioid and surirelloid genera is remarkably low. In fact, there are almost as many new taxa of Neidium (23 taxa), a genus of relatively restricted ecological distribution, described from the U.S. as there are taxa of the more eurytolerant (at the level of genus) Nitzschia (24 taxa). These discrepancies must be attributable to the lack of monographs on these genera. Genera that are only known in the U.S. flora include Plavaensis Spaulding \& Kociolek, Sarcophagodes Morales and Pseudostaurosiropsis. Absence of reports from other areas may be due to their relatively recent discovery.

In terms of geography, the areas supporting the most new taxa are Oregon (83 taxa), Pennsylvania (52 taxa), Florida (51 taxa), South Carolina (49 taxa) and the state of Washington (36 taxa). While Oregon and Washington, as well as Florida might be seen as unique areas, somewhat surprising is the relatively large number of taxa described from the eastern coastal plain. Of course, these areas have received the greatest amount of attention from diatomists, especially South Carolina, and the Savannah River, which have been monitored heavily due to the presence of a nuclear power plant. The bottom line is areas that receive any detailed attention have been found to bear new taxa, and this is emphasized by the work on the Laurentian Great Lakes, Iowa, and the east coast of the U.S. also showing many taxa being described from those areas. Lack of new taxa from many parts of the U.S. is due probably more to lack of attention than lack of interesting species. It is still the situation that some of the lists developed by Ehrenberg (1854) for parts of the Deep South are in fact the only published information on freshwater recent diatoms from the area.

Table 1 also reminds us how many taxon names we do not see referenced in the current literature. While most taxonomists know of the works of Patrick and Reimer, it may be surprising that more species have been described from the continental United States by the late Matthew Hohn ( 72 taxa) than either Ruth Patrick (47 taxa) or Charles Reimer (40 taxa), yet few of the taxa authored by Hohn are noted in the U.S. flora. Likewise, species such as Cocconeis patrickae Reimer and Navicula daileyi Reimer, both known from Indiana, are rarely reported. This lack of reporting of these names is due to the fact that the work of Hohn and these names of Reimer were not included in the flora of Patrick and Reimer $(1966,1975)$. Descriptions of new taxa in the primary literature do not readily, if at all, get into the parlance of practicing taxonomists. Thus, the need for a new U.S. flora is underscored to summarize and make more accessible the vast data on the diatom flora of freshwaters in the U.S., especially that information in the primary literature that has accumulated for more than 40 years since Patrick and Reimer reviewed and incorporated the primary literature into a flora.

## Conclusions

Although we have come a long way in our studies of the diatom flora of the U.S., we are far from achieving a complete understanding. The obstacles to gaining a fuller understanding are difficult, and the time, people, and financial resources to gain such knowledge are daunting. I must say, however, that the development of a U.S. flora will be modest in cost relative to the utility of the work and the amount being spent on projects that are operating without such a basic tool.

In addition to the taxonomic infrastructure that is being put into place that could be used to great benefit in the development of a U.S. freshwater diatom flora, there are also some advances in
other research tools that could facilitate a project of this scope. One example can be found dealing with the freshwater diatoms of south Florida (http://serc.fiu.edu/periphyton). These tools should include mature structures of complex databases that support the organization and sharing of information both internally and with collaborators across the country and the world. These are already used by ANSP and CAS to organize the material, slides and identifications for internal use, and for searching by external users, but also facilitate input from individuals outside the institutions (see the system in place at ANSP at http://www.diatom.acnatsci.org/AlgaeImage).

Perhaps one of the greatest leaps in the development of species descriptions, monographs, taxonomic revisions and floras in the last 20 years has been documentation of variability within a taxon. This has been done by incorporating many micrographs into the work (examples include Kociolek and Stoermer 1988, Krammer and Lange-Bertalot 1986-1991; Krammer 2003). This approach has been facilitated in more recent times by the development of digital imaging, where publication-quality images can be received directly from microscope to computer, without the timeconsuming process of artists drawing the specimen or the processing of film and printing of prints. In the development of a modern flora, this is by far one of the best timesaving devices.

No one laboratory, probably no one institution, can alone do this work within a reasonable time frame. Such a task will require a team of taxonomic experts. It will involve accessing materials from numerous herbaria, and a complicated management plan so that the large task of evaluating and synthesizing past work can happen, but also allowing time for a "discovery" effort to occur.

A modern flora will of necessity be a flexible and up-datable system (for a similar view, see Wheeler et al. 2004) that is distributed, such that it can support a team of collaborators and be applied by an international body of users. A flora then is an information system, in this case for the freshwater diatoms of the U.S. It requires a well thought-out framework for information capture and management (i.e. database), which supports potentially a wide range of users. Though such an approach can require time to develop and populate with data, it can result in reproducible results (because data are tied to specimens that can be reviewed by future workers), and allow the basic information to be leveraged across a variety of fields for research and educational uses. It seems to me that we can build on the great body of work that has been accomplished over the last 150 years, including the floras that have been developed previously. With the legacy of previous workers whose collections have been maintained and are accessible for study by current (and future) generations, and the near completion of important research tools, we are well positioned to commence immediately and realize this important work.

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## References

Balley. J.W. 1851. Microscopical observations made in South Carolina. Georgia and Florida. Smithsonian Contributions to Knowledge 2:1-48.
Barber. H.G. and Haworth. E.Y. 1981. A guide to the morphology of the diatom frustule, with a key to the British freshwater genera. Freshwater Biological Association, Scientific Publication 44:1-112.

Boyer. C.S. 1927a. Synopsis of the North American Diatomaceae. Proceedings of the Academy of Natural Sciences of Philadelphia 78:1-228.
Boyer, C.S. 1927b. Synopsis of the North American Diatomaceae. Proceedings of the Academy of Natural Sciences of Philadelphia 78:229-583.
Camburn, K.E. 1982. The diatoms (Bacillariophyceae) of Kentucky: A checklist of previously reported taxa. Transactions of the Kentucky Academy of Sciences 43:1-20.
Camburn, K.E. and Charles, D.F. 2000. Diatoms of Low-alkalinity Lakes in the Northeastern United States. Special Publication 18, Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA. 152 pp.
Camburn, K.E., Kingston, J.C. \& Charles, D.F. [Eds]. 1984-1986. PIRLA Diatom Iconograph. PIRLA Unpublished Report Series, Report 3. Electric Power Research Institute. 53 plates, 1059 figures.
Chase, H.H. 1885. Habirshaw's Catalogue of the Diatomaceae. Privately printed by author, Geneva, New York, USA. 343 pp.
Chase, H.H., ed. 1907. Index Diatomacearum. Privately printed by author, Linden, Michigan, USA. 662 pp.
Collins, G.B. and Kalinsky, R.G. 1977. Studies on Ohio diatoms:II. Referenced checklist of diatoms from Ohio exclusive of Lake Erie and the Ohio River. Bulletin of the Ohio Biological Survey 5:46-76.
Dixit S.S. And Smol J.P. 1994. Diatoms as indicators in the Environmental Monitoring and Assessment Program-Surface Waters (EMAP-SW). Environmental Monitoring and Assessment 31(3):275-306.
Dodd, J.J. 1987. Diatoms. The Illustrated Flora of Illinois. Southern Illinois University Press, Carbondale, Illinois, USA. 478 pp.
Ehrenberg, C.G. 1854. Mikrogeologie. Das Erden und Felsen schaffende Wirken des unsichtbar kleinen selbständingen Lebens auf der Erde. Leopold Voss, Leipzig. Germany. 374 pp.
Elmore, C.J. 1922. The diatoms (Bacillarioideae) of Nebraska. Nebraska Geological Survey 8:1-216.
Fourtanier, E. and Kociolek, J.P. 1999. Catalogue of diatom genera. Diatom Research 14:1-190.
Habirshaw, F. 1877. Catalogue of the Diatomaceae with Reference to the Various Published Descriptions and Fgures. Reproduced by Edison Electric Pen Process, New York, New York, USA. 272 pp.
Hohn, M.J. and Hellerman, J. 1963. The taxonomy and structure of diatom populations from three eastern North American rivers using three sampling methods. Transactions of the American Microscopical Society 82:250-329.
Kingston, J.C., Lowe, R.L., Stoermer, E.F., and Ladewski, T.B. 1983. Spatial and temporal distribution of benthic diatoms in northern Lake Michigan. Ecology 64:1566-1580.
Kociolek, J.P., Mahood, A.D., and Nutile, K. 1999. The types of the Diatom Collection of the California Academy of Sciences. Pages 157-196 in S. Mayama, K. Idea \& I. Koizumi, eds., Proceedings of the 14th International Diatom Symposium. Koeltz Scientific Books, Koenigstein, Germany.
Kociolek, J.P. and Spaulding, S.A. 2003. General introduction to the diatoms. Pages 559-562 in J. Wehr \& R. Sheath, eds., Freshwater Algae of North America, Chapter 15. Academic Press, San Diego, California, USA. 918 pp .
Kociolek, J.P. and Stoermer, E.F. 1988. Taxonomy, ultrastructure, and distribution of Gomphoneis herculeana, G. eriense and closely related species. Proceedings of the Academy of Natural Sciences of Philadelphia 140:24-97.
Kociolek, J.P. and Stoermer, E.F. 2001. Taxonomy and ecology: A marriage of necessity. Diatom Research 16:433-442.
Krammer, K. 1992. Pinnularia. Die Gattung Pinnularia in Bayern. Hoppea 52:1-308.
Krammer, K. 1997a. Die cymbelloiden Diatomeen. Eine Monographie der weltweit bekannten Taxa. Teil 1. Allgemeines und Encyonema Part. Bibliotheca Diatomologica 36:1-382.
Krammer, K. 1997b. Die cymbelloiden Diatomeen. Eine Monographie der weltweit bekannten Taxa. Teil 2. Encyonema part, Encyonopsis und Cymbellopsis. Bibliotheca Diatomologica 37:1-469.
Krammer, K. 2000. The genus Pinnularia. In: H. Lange-Bertalot, ed., Diatoms of Europe, Volume 1. A.R.G. Gantner, Ruggell, Germany. 703 pp.
Krammer, K. 2002. Cymbella. In: H. Lange-Bertalot, ed., Diatoms of Europe, Volume 3. A.R.G. Gantner, Ruggell, Germany. 584 pp.
Krammer, K. 2003. Cymbopleura, Delicata, Navicymbula, Gomphocymbellopsis, Afrocymbella. In: H. Lange-

Bertalot, ed., Diatoms of Europe, Volume 4. A.R.G. Gantner, Ruggell, Germany. 530 pp.
Krammer, K. and Lange-Bertalot, H. 1986. Bacillariophyceae. Teil 1. Naviculaceae. In: H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer, eds., Süsswasserflora von Mitteleuropa, Band 2. G. Fisher, Stuttgart, Germany. 876 pp .
Krammer, K. and Lange-Bertalot, H. 1988. Bacillariophyceae. Teil 2. Bacillariaceae, Epithemiaceae, Surirellaceae. In: H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer, eds., Süsswasserflora von Mitteleuropa, Band 2. G. Fisher, Stuttgart, Germany. 596 pp.
Krammer, K. and Lange-Bertalot, H. 1991a. Bacillariophyceae. Teil 3. Centrales, Fragilariaceae, Eunotiaceae. In: H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer, eds., Süsswasserflora von Mitteleuropa, Band 2. G. Fisher, Stuttgart, Germany. 576 pp.
Krammer, K. \& Lange-Bertalot, H. 1991b. Bacillariophyceae. Teil 4. Achnanthaceae. Kritische Erganzungen zu Navicula und Gomphonema. In: H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer, eds., Süsswasserflora von Mitteleuropa, Band 2. G. Fisher, Stuttgart, Germany. 437 pp.
Lange-Bertalot, H. 2001. Navicula sensu stricto, 10 genera separated from Navicula sensu stricto, Frustulia, In: H. Lange-Bertalot, ed., Diatoms of Europe, Volume 2. A.R.G. Gantner, Ruggell, Germany. 526 pp.
Lange-Bertalot, H., Külbs, K., Lauser, T., Nörpel-Schempp, M. \& Willmann, M. 1996. Diatom taxa introduced by Georg Krasske - documentation and revision. Iconographia Diatomologica 3:1-358.
Lange-Bertalot, H. and Moser, G. 1994. Brachysira. Monographie der Gattung. Bibliotheca Diatomologica 29:1-212.
Mahoney, R.K. and Reimer, C.W. 1997. Updated status of the type collection (Bacillariophyceae) in the Diatom Herbarium, The Academy of Natural Sciences of Philadelphia. Proceedings of the Academy of Natural Sciences of Philadelphia 147:125-192.
Mills, F.W. 1933-1935. An Index to the Genera and Species of the Diatomaceae and Their Synonyms, 1816-1932. Wheldon and Wesley, London, UK. 1726 pp.
Moser, G., Lange-Bertalot, H. and Metzeltin, D. 1998. Insel der Endemiten. Geobotanisches Phänomen Neukaledonien. Bibliiotheca Diatomologica 38:1-464.
Patrick, R.M. 1959. Bacillariophyceae. Pages 171-189 in W.T. Edmonson, ed., Freshwater Biology, Second Edition. J. Wiley, New York, New York, USA. 1248 pp.
Patrick, R.M. 1961. A study of the numbers and kinds of species found in the rivers in eastern United States. Proceedings of the Academy of Natural Sciences of Philadelphia 113:215-258.
Patrick, R.M. and Reimer, C.W. 1966. The Diatoms of the United States, Volume 1. Monograph 13. Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA. 688 p.p.
Patrick, R.M. and Reimer, C.W. 1975. The Diatoms of the United States, Volume 2, Part 1. Monograph 13. Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA. 213 pp.
Paulsen, S.G. and Linthurst R.A. 1994. Biological monitoring in the Environmental Monitoring and Assessment Program. Pages 297-322 in S.L. Loeb and A. Spacie, eds., Biological monitoring of aquatic systems. Lewis Publishers, Boca Raton, Florida, USA.
Peragallo, M. 1897-1903. Le Catalogue général des Diatomées. Paris (1897; xviii + $471+$ [1 \{Additions \}]) and Clermont-Ferrand (1903; 472-973 + [4 \{Additions\}]), France. xviii $+973+(5)$ pp.
Porter, S.D., Cuffney, T.F., Gurtz, M.E., and Meador, M.R. 1993. Methods for Collecting Algal Samples as part of the National Water-Quality Assessment Program. U.S. Geological Survey-Open File Report 93409. Raleigh, North Carolina, USA. 39 pp.

Potapova, M.G. and Charles, D.F. 2002. Benthic diatoms in USA rivers:distributions along spatial and environmental gradients. Journal of Biogeography 29:167-187.
Prescott. G.W. and Dillard. G.E. 1979. A checklist of algal species reported from Montana 1891 to 1977. Monograph No. 1. Proceedings of the Montana Academy of Sciences (Supplement) 36:1-102.
Reichardt, E. 1995. Die Diatomeen (Bacillariophyceae) in Ehrenbergs Material von Cayenne, Guyana Gallica (1843). Iconographia Diatomologica 1:1-53.
Reichardt, E. 1999. Zur Revision der Gattung Gomphonema. Die Arten um G. affine/insigne, G. angustatum/micropus, G. acuminatum sowie gomphonemoide Diatomeen aud sem Oberoligozän in Böhmen. Iconographia Diatomologica 8:1-203.
Reichardt, E. and Layge-Bertalot, H. 1991. Taxonomische Revision des Artenkomplexes um Gomphonema
angustatum-G. dichotomum-G. intricatum-G.vibrio und ähnlicher Taxa (Bacillariophyceae). Beihefte zur Nova Hedwigia 53:519-544.
Rushforth, S.R. and Squires, L.E. 1985. New records and comprehensive list of the algal taxa of Utah Lake, Utah, USA. Great Basin Naturalist 45:237-254.
Simonsen, R. 1987. Atlas and Catalogue of the Diatom Types of Friedrich Hustedt. 3 Volumes. J. Cramer, Berlin, Germany.
Sorereign, H.E. 1963. New and rare diatoms from Oregon and Washington. Proceedings of the California Academy of Sciences, ser. 4, 31:349-368.
Stoermer, E.F. 1981. Diatoms associated with bryophyte communities growing at extreme depths in Lake Michigan. Proceedings of the Iowa Academy of Sciences 88:91-95.
Stoermer, E.F. and Kreis, R.G., Jr. 1978. Preliminary checklist of diatoms (Bacillariophyta) from the Laurentian Great Lakes. Journal of Great Lakes Research 4:149-169.
Stoermer, E.F., Kreis, R.G., Jr. and Andresen, N.A. 2000. Checklist of diatoms from the Laurentian Great Lakes II. Journal of Great Lakes Research 25:515-566.
The Times Comprehensive Atlas of the World, 11th ed.. 2005. Harpe Collins, UK. 544 pp.
U.S. Environmental Protection Agency. 1975. National Eutrophication Survey Methods 1973-1976. Working Paper No. 175. Environmental Support Laboratory, Las Vegas, Nevada and Corvallis Environmental Research Laboratory, Corvallis, Oregon, USA. 91 pp.
Vax Landingham, S.L. 1967-1979. Catalogue of the Fossil and Recent Genera and Species of Diatoms and Their Synonyms. J. Cramer, Lehre, Germany.
Vinyard, W.C. 1979. Diatoms of North America. Mad River Press, Eureka, California, USA. 119 pp.
Wheeler, Q.D., Raven, P.H., and Wilson, E.O. 2004. Taxonomy:Impediment or expedient. Science 303:285.
Wehr, J.D. \& Sheath, R.G., eds. 2003. Freshwater Algae of North America. Ecology and Classification. Academic Press, San Diego, California, USA. 918pp.
Wileiams, D.M. 1985. Morphology, taxonomy and inter-relationships of the ribbed araphid diatoms from the genera Diatoma and Meridion (Diatomaceae:Bacillariophyta). J. Cramer, Vaduz, Germany. 255 pp.
Wrliams, L.G. and Scott, C. 1962. Principal diatoms of major waterways of the United States. Limnology and Oceanography 7:365-379.
Wolle, F. 1890. Diatomaceae of North America. Comenius Press, Bethlehem, Pennsylvania, USA. 42 pp.

TAble: I. Listing of taxa, type locality and types (type designation, institution, and slide number) of diatoms described as new to science for the United States. $\mathrm{H}=$ holotype: I=isotype; Icono=Iconotype; $\mathrm{I}=l$ letotype; $\mathrm{ANSP}=$ Academy of Natural Sciences of Philadelphia; $\mathrm{B}=$ Botanical Museum, Berlin, Dahlem; BIHUPM=Humboldt University Patcontological Muscum, Berlin: BM=British Museum. London: BRM=Alfred Wegener Institute, Bremerhaven; CAS=California Academy of Sciences; NAU=Northern Arizona University, Flagstaff; NW=Naturhistorisches Museum, Wien; USNM=U.S. National Museum |National Museum of Natural History, Washington, D.C.J; IOK=Collection of K. Krammer; ILL= Iowa Lakeside Lab Collection; ISU=Herbarium of Iowa State University; Lange-Bertalot=Collection of H. Lange-Bertalot at G.W. Goethe-Institute, Frankfurt, Germany; VH=Van Heurck Collection, Antwerp:

Taxel Ac/mammhes americama Cleve 1895

Achmamthes biporoma Hohn \& Hellerman 1963

Achnamthes alecipic'ms Reimer 1906
Achmamthe's deflexa Reimer in Patrick \& Reimer 1966 Aclunamthes deflexa var. alpestris Lowe \& Kociolck 1984 Achuanthes detha Hohn \& Hellerman 196.3 Achnamthes harveyi Reimer 1960

Ichunamhes hanceolata var. apictulate Patrich Paick \& Reimer 1966 Achncumhes

Aclmumhes lewisiana Patrick
1963
chmumines oserupii var. perwerla Paltrick 1945
Achnanthes peragalli var. fossilis Tempère \& Peragatlo
Aclmanthes prava Sovereign
le'mnculthes reimeri Camburn uerman 1963
1961
Achucuthes sewurii Patrick
Achmanthes sublaevis var. crassa Reimer in Paltrick \& Reimer 1966 Achnamthes subrostrata var. appalachiana Camburn \& Lowe 1979

Achnanthes temperei Peragallo in Tempère \& Peragallo
Lange-Bertalot \& Krammer 1989
NII: Pennichuck Brook
NII: Saco Pond

H:ANSP:57579; I:CAS:221(075
L:ANSP:Febiger 2372
H:ANSP:I05793:
H:ANSP:44483 (Hohn says "44484")
H:ANSP:44469
H:CAS:Stoermer 1545
H:CAS:Stoermer 1574
H:CAS:Stoermer 1258
H:ANSP:44466
H:CAS:Stoermer 1165
H:CAS:Stoermer 1520
H:ANSP:8027
H:CAS:Stoermer 1565 H:CAS:Stoermer 1565 H:I.L.L.:SP33
H:ANSP:Boyer 818 H:ANSP:45101 H:BRM:Nd/83 N:ANSP:Boyer 392 H:CAS:216060

H:ANSP:57551 H:ANSP:2018 H:BRM:N6/92 H:ANSP:44484
OH: Lake Erie, Clevelans
OR: Multnomah Co., Willamette River
TX: Comale Creek
FL: Withlacoochee River
FL: Silver Springs
PA: Ridley Creek
Lake Michigan
Lake Michigan
Lake Michigan
Lake Michigan
MD: Potomac River
MI: Cheboygan Co., Douglas Lake
Between Lake Michigan and Lake Macatawa
TX: Orange Co., Sabine River
Lake Michigan
IA: Dickinson Co., Excelsior Fen
NJ: Ocean Co., Toms River
FL: Santa Rosa Co., $11 / 2$ miles NE of Milton
Several localities including NY and MA
AL: Mobile
NH: Carroll Co., Bemis Lake
CA: Mono Lake
MI: Schoolcraft Co., Cusino Lake
OR: Columbia River RI: Newport, Northam's Pond NY: Staten Island, Clifton
NY: Hudson River at West Point
WA: Tacoma
FL: Silver Springs

H:BRM:N6/92

| New England; Merrimac River, on Chara |  |
| :---: | :---: |
| OR: Lower Klamath Lake, Lost River |  |
| ND: Devil's Lake | L:ANSP:Boyer X-V-1 |
| MI: Ttuabawassee R. al Midland | H:ANSP:53766 |
| FL: Silver Springs | H:ANSP:44474 |
| FL: Silver Springs | H:ANSP:44489 |
| SC: Allendale Co., Savannah River | H:ANSP:3872b |
| FL: Silver Springs | H:ANSP:44474 |
| OR: Upper Klamath Lake | H:CAS:205074 |
| IN: Randolph Co., Cabin Creek bog | H:ANSP:45669 |
| FL |  |
| OR | H:CAS:205075 |
| NY: Genesee Co., Bergen Swamp | H:Wiegand Herb. Cornell:162 |
| IA: Dickinson Co.. W. Lake Okoboji, Lazy Lagoon | H:ANSP:63787 |
| TX: Hardin Co., Neches River | H:ANSP:8024 |
| America |  |
| Lake Michigan |  |
| Lake Michigan |  |
| TX: Hardin Co.. Neches River | H:ANSP:8102 |
| WA: San Juan Co., Orcas Island, Lake Killebrew | H:CAS:205087 |
| Lake Michigan |  |
| SC: Barnwell Co. L Lake | H:ANSP:55688 |
| OR: Klamath Co.. Swan Lake | I:CAS/ANSP: T \& P (2) 365, 366 |
| MA: Waltham, Crane Pond |  |
| RI: North Providence |  |
| ID: Oreana, Pickett Creek | H:IOK:808B |
| IN: Randolph Co., Cabin Creek bog | H:ANSP:45669 |
| OR: Klamath Co., Swan Lake | I:CAS/ANSP: T \& P (2) 365, 366 |
| WA: King Co., Shadow Lake | H:CAS:206006 |
| OR: Klamath Co., Swan Lake | I:CAS/ANSP: T \& P (2) 365, 366 |

Caloneis sperciosa (Hustedt) Bay
Capartogramma crucicula (Grunow) Ross
Capartogramma crucicula (Grunow) Ross
Cestodiscus baileyi H.L. Smith 1878
Cestodiscus baileyi H.L. Smith 1878
C'haetoceros elmorei Boyer 1914
Chaetoceros hohnii Gracbner \& Wujek
Cocconeis delalineata Hohn 1961
Cocconeis delapunctata Ilohn 1961
Cocone's flatiatilis Watace
Cocconeis inusitatus Ilohn 1961
Cocconeis klamathensis Sovereign
Cocconeis patrickiae Remer 1961
Cocconeis placentula var: euglypra (Ehrenterg) (Yeve
Cocconeis rugosa Sovereign 1958
Coscinodiscus subtilis var. radiant
Coscinodiscus subtilis var: radiatus Hohn 1952
Cyclostephanos tholiformis Stoermer et al. 1987
Cyclotella aliquantula Hohn \& Hellerman 1963
Cyclotella americana Fricke
Cyclotella bodanica var: michiganensis Skvortzow 1937
Cyclotella bodanica var: stellata Skvortzow 1937
Cyclotella facetia Hohn \& Hellerman 1963
Cyclotella gamma Sovereign
Cyclotella michiganiana Skvortzow 1937
Cyclotubicoalistus undatus Stoermer et al. 1990
Cymatopleura manmii M. Peragallo in Tempère \& Peragallo 1909
Cymbella acutiuscula Cleve 1894
Cymbella americana A.Schmidt 1885
Cymbella buechleri Krammer 2002
Cymbella cesati var. linearis Reimer 1961
Cymbella cistula var. crassa Tempère \& Peragallo 1909
Cymbella couleensis Sovereign
Cymbella cucumis var. delicata Tempère \& Peragallo1909
I:CAS/ANSP: T \& P (2) 365, 366
H:IOK:799
H:IOK:808B
H:IOK:808B
L:BRM:T2/24
L:ANSP H.L. Smith 72-641
H:BRM:TI/72
H:USNM:20560
H:ANSP:6590a
L:ANSP T \& P 524
H:BRM:T2/4
H:IOK:812
H:BRM:T2/17
H:ANSP:1909
H:CAS:206007
H:IOK:808B
H:ANSP:57555

## I:ANSP:H.L. Smith B-85

H:CAS:206008
I:CAS/ANSP: T \& P (2) 728, 729
L:ANSP T \& P (2) 104

\section*{I(?):ANSP: T \& P (1) 104

\section*{H:IOK:1068C

## H:IOK:1068C <br> L:ANSP:H.L. Smith 72-641 <br> I:BRM:T1/51(?) I:CAS/ANSP: T \& P (2): 365,366 H:IOK:1042C L:ANSP:T \& P (1): 524

|WA|: Fort Ludlow OR: Klamath Co., Swan Lake
UT: Zion National Park
ID: Oreana, Pickett Creek
ID: Oreana, Pickett Creek
OR: Pitt River
CA: Honey Lake Valley
OR: Oregon River
ME: Cherryfield
CA: San Francisco
CT: New Haven
NM: Rio Arriba Co.
CA: San Francisco
TX: Guadalupe Co., Guadalupe River
NJ: Weequachick Lake
OR: Columbia River
OR: Terrebone
OR: Columbia River
IN: Marshall Co., Lake Maxinkuckee
WA: Mt. Rainier National Park, Mowich Lake
ID: Oreana, Pickett Creek
NY: Franklin Co., Grass Pond
NY: "Vivum in Niagara"
CA: Suisun Bay
WA: Mt. Rainier National Park,

## MA: Pellham <br> CT: Plymouth, Todd Hollow CT: Hartford Co., Bristol, Fall Mountain <br> CT: Bristol, Fall Mountain

FL: Everglades
CA: Honey Lake Valley
KY: Mammoth Cave National Park
OR: Pitt River, Fall River
FL: Everglades
NJ: Weequachick Lake
 Cymbella triangulum (Ehrenberg) Cleve
Diatoma anceps (Ehrenberg) Kirchner Diatoma anceps var. constricta Tempère \& Peragallo 1912 Diatoma anceps var. linearis M. Peragallo
Encyonema 1909 Encyonema silesiacum var. elegans Krammer 1997a Encyonema temperei Krammer 1997b
[WY]: Yellowstone National Park, Geyser 2
OR: Terre Bone
[NY]: "Vivum in Niagara"
NJ: Weequachick Lake
[WY]: Yellowstone National Park, Firehole River
FL: Clermont
|NH]: Bemis Lake, White Mountains
[WY|: Yellowstone National Park
NH: Bemis Lake, White Mountains
NH: Bemis Lake, White Mountains
NH: Bemis Lake, White Mountains
ME: Cherryfield
FL: Withlacoochee River
FL: at Enterprise
WI: Jackson Co., Trempealeau Valley OR: Klamath Co., Swan Lake OR: Klamath Co., Swan Lake OR: Klamath Co., Swan Lake OR: Klamath Co., Swan Lake

ME: Blue Hill Pond Great Smoky Mountains National Park GA: Mouth of Upper Three Runs OR: Columbia River LA: Bossier Parish, Cyp OR: Columbia River NV: Kings River OR: Columbia River OR: Columbia River OR: Columbia River NJ: Atlantic City OR: Columbia River OR: Columbia River OR: Columbia River OR: Columbia River OR: Columbia River AL: Mobile, Spring Hill
FL: at Enterprise

H:BRM:T3/100
H:IOK:833 L.ANSP.T \& P (1): 524
L:ANSP:T \& P (1): 524
H:IOK:1032; I:IOK:1033
H:IOK:804
H:VH:544
H:IOK:1044
L:VH:Cleve \& Moller 274
H:IOK:1173F
L:VH:Cleve \& Moller 274
H:VH:Cleve \& Moller 168 L:ANSP:T \& P (2) 366
L:ANSP:T \& P (2) 366
L:ANSP:T \& P (2) 366
I:CAS/ANSP: T \& P (2) 365, 366 I:CAS/ANSP: T \& P (2) 365, 366 H:ANSP:53917
H:ANSP:44254a
L:BRM:X11/37
H:ANSP:53901
L:BRM:X11/33
L:BRM:239/63
L:BRM:X11/37
L:BRM:L3/12
L:BRM:X11/37
H:BRM:L2/26 L:BRM:X11/37 L:BRM:X11/33 L:BRM:X11/37

## L:BRM:X11/37 <br> H:CAS:NY Ward C-7-17-N

| NY: West Point |  |
| :---: | :---: |
| SC: Barnwell Co., shallow Carolina Bay | H:ANSP:57542a |
| USA |  |
| USA |  |
| NY: Hamilton Co., Queer Lake | H:ANSP:57553 |
| OR: Columbia River | L:BRM:L3/5 |
| NV: Kings River | L:BRM:239/63 |
| SC: Barnwell Co, shallow Carolina bay | H:ANSP:57543: |
| OR: Columbia River | L:BRM:L3/60 |
| MA: Taunton | H:BRM:LI/15 |
| FL: Silver Springs | H:ANSP:44474 |
| LA: Bossier Parish, Cypress Bayou Res. | H:ANSP:53902 |
| OR: Klamath Co., Swan Lake | I:CAS/ANSP: T \& P (2) 365, 366 |
| NY: Croton River |  |
| OR: Diamond Lake | H:CAS:205072 |
| PA: Ridley Creek | H:ANSP:44458 |
| FL |  |
| MD: Potomac River | H:ANSP:44467 |
| FL: Silver Springs | H:ANSP:44474 |
| PA: Ridley Creek | H:ANSP:44469 |
| WA: Tacoma | I:CAS/ANSP: T \& P (2) 107, 108 |
| PA: Ridley Creek | H:ANSP:44471 |
| FL: Pensacola | L:BRM:Ka/7 |
| OR: Klamath Co., Swan Lake | L:ANSP:T \& P (2) 366 |
| NY: Herkimer Co., Buck Pond | H:ANSP:57552 |
| FL: Everglades | H:Lange-Bertalot, BIUFaM:Am-N 66 |
| IA | H:ISU:7-4-69 \#2 |
| NJ |  |
| NC: Hayward Co., Flat Laurel Gap Bog | H:ANSP:56842 |
| NY: Herkimer Co., Fourth Lake (Bisby Lakes) | H:ANSP:57556 |
| OR: Crater Lake National Park, Water Supply Spring | H:CAS:205089 |
| CA: Shasta |  |
| Lake Erie |  |
| OR: Emerald Pool, Crater Lake | H:CAS:Sovereign 488-1 |
| IA: Dickinson Co., Lake W. Okoboji | H:I.L.L.:L-2-12 |
| CA: Pitt River |  |
| MT: Bitteroot River | H:ANSP:64382 |

E:unotia pectinalis var. ventricosa Grunow
timnotia praterupta lihrenberg
t:unotia pracrupta var: bidens (Bhrenberg) Grunow Eiunotia punctastriatum Camburn \& Charles 2000 Eunotia recta Husied 1913
Eunotia rostellata Ilustedt ex Patrick 1945
Eunotia serraceniae Gaiser \& Johansen 2000 Eunotia submonodon Hustedt 1913 Eunotia taumtomiensis Hustedt
Eunotia torula Holm 1961
Eunotia zasuminensis var. minor Kalinsky 1984
Fragilaria aequalis var. major Tempère \& Peragallo 1090 Fragilaria crotonensis Kitton
Fragilaria crotonensis var. oregona Sovereign
Fragilaria dibolos Hohn \& Hellerman 1963
Fragilaria floridana Hanna
ragitaria
Fragilaria gnathostoma Hohn 1961
Fragilaria interstincta Hohn \& Hellerman 1963
Fragilaria marina var. parva Tempère \& Peragallo Fragilaria rhodana Hohn \& Hellerman 1963 Fragilaria robusta Hustedt
Fragilaria sinuata M. Peragallo
Fragilaria suboldenburgiana Camburn \& Charles 2000 Fragilaria synegrotesca Lange-Bertalot 1993 Fragilaria vaucheriae f. contorta Lowe 1972

## Frustulia asymmetrica (Cleve) Hustedt

 Frustulia asymmetrica (Cleve) HustedtFrustulia bahlsii Edlund \& Brant 1997
Frustulia pseudomagaliesmontana Camburn \& Charles 2000 Frustulia rhomboides f. occidentalis Sovereign
Gomphoneis elegans (Grunow) Cleve Skwor
Gomphoneis elegans (Grunow) Cleve
Gomphoneis eriense (Grunow) Skvortz Gomphoneis eriense var. angularis Kociolek \& Stoermer 1988 Gomphoneis eriense var. apiculata Stoermer in Reimer 1982 Gomphoneis eriense var. rostrata (M. Schmidt) Skvortzow
in Skvortzow \& Meyer
Gomphoneis eriense var. variabilis Kociolek \& Stoermer 1988
H:CAS:216020
H:Humboldt-Berlin 1754; I:Farlow 1967
H:ANSP:64380
H:ANSP:64380
H:CAS:Sovereign 488-1 S:ANSP:Cl. \& Moll. 40 I:CAS?ANSP: T \& P (2) 365, 366
H:CAS:216019;Kociolek \& Stoermer 1991 H:ANSP:T \& P (2) 3666 H:ANSP:64381

## H:B:S1838-T01

## I:CAS/ANSP:T \& P (2): 103,104 H:ANSP:4242b H:ANSP:53920 H:ANSP:44458 H:ANSP:44458

 H:Humboldt-Berlin 1754; I:Farlow 1967H:CAS:Ward F-188-1 H. CAS. 218005 H:CAS:216016 H:ANSP:53900 H:B:S1838-T01 I:ANSP:T\&P 887 H:ANSP:54754 H:CAS1131 H2-N H:CAS:216015
MN: Cook Co., Lake Superior
Lake Huron: Mackinaw Island
CA/NV: Lake Tahoe, Sunnyside
OR: Pitt River (probably CA)
OR: Emerald Pool, Crater Lake
NY
OR: Klamath Co., Swan Lake
OR: Jefferson Co., Metolius River
OR: Fall River
Lake Superior
OR: Swan Lake
OR: Swan Lake
OR: Lane Co., W. Odell Lake
OR: Lane Co., Linton Lake
UT: Washington Co., Spring at Zion National Park
CT: Bristol, Fall Mountain
NY
A. Wort Co., Bis Creck
Great Smoky Mountains National Park, Big Creek
PA: Ridley Creek
MA: Waltham; RI:
PA: Ridley Creek
$\mathrm{H}:$ ANSP:44458
$H:$ ANSP:53921
H:CAS:216008
$H: A N S P: 4356 a$

| H:ANSP:62242 |  |
| :---: | :---: |
|  | H:ANSP:44468 |
| H:ANSP:53755 |  |
|  | H:B:S1840-T01 |
| H:CAS:216018 |  |
| H:CAS:216017 |  |
| H:ANSP:53756 |  |
| H:CAS:216014 |  |
| H:CAS:Stoermer 1867 Icono:Ehrenberg, Mikrogeologie, p. 15, pl. IV,2, fig. 34; |  |
|  |  |
| BHUPM:Kasten 26, Buch 5, Mica-Streifen 8, Mica |  |
| NR 2 |  |
| H:ANSP:57551 |  |
| H: CAS: 205086 |  |
| L:ANSP:Boyer W-VI-20 L:ANSP:Boyer W-VI-17 I:ANSP:3174 |  |
|  |  |
|  |  |
| H:ANSP:2861 <br> L:ANSP:Boyer W-VI-14 |  |
|  |  |
| I:CAS/ANSP: T \& P (2) 103, 104 |  |
| H:BRM:R1/89 |  |
| H:ANSP:54241 |  |
| H:ANSP:54240 |  |
| H:ANSP:54239 |  |
| H:ANSP:54238 |  |
|  | H:ANSP: 57560 |

NY: West Point
MI: Schoolcraft Co., Cusino Lake
OR: Crater Lake
OH: Columbus
OH: Columbus
NY: Croton River
CT: "Eaux saumatres"
FL: Green Spring
OH: Columbus CT: Bristol, Fall Mountain
CT: Morris Cove
WI: Oneida Co., Dorothy Lake
MI: Alger Co., Sand Lake
MI: Chippewa Co., McNearney Lake

NC: Avery Co., Sugar Mountain Bog


OH : Columbus
MI: Schoolcraft Co., Cusino Lake
(iomphonema semiapertum Grunow
Gomphonema sepum Moghadam
Gomphonema simus Hohn \& Hellerman 1963
(iomphonema sparsistriatum I: maculatum Camburn 1978
Gomphomema sphucrophorum Ehrenberg
Gomphonema stonei Reichard 1999
Gomphonema submeheri Kociolek \& Stoermer 1991
Gomphonema subtile Ehrenberg
Gomphonema superiorensis Kociolek \& Stoermer 1991
Gomphonema tackei var. bre vistriatum Camburn 1978
Gomphonema truncatum var. macilentum Kociolek \& Stoermer 1991
Gomphonema truncatum var. turgidum (Ehrenberg) Patrick
Gomphonema tumens Kociolek \& Stoermer 1991
Gomphonema turgidum Grunow

## Gomphonema turris Ehrenberg

Gomphonema variostriatum Camburn \& Charles 200
Gomphonitzschia exigua Sovereign 1958
Gyrosigma obtusatum (Sullivan \& Wormley) Boyer Gyrosigma sciotense (Sullivan \& Wormley) Cleve Gyrosigma spencerii (Quekett) Griffen \& Henfrey Gyrosigma temperei Cleve Gyrosigma terryanum f. fontanum Reimer Gyrosigma wormleyi (Sullivant) Boyer Hantzschia vivax var. granulata M. Peragallo in Tempère \& Peragallo 1908

Mastogloia angusta Hustedt 1933
Melosira distans var. nivaloides Camburn 1986 Melosira nygaardii Camburn 1986 Melosira perglabra var. floriniae Camburn 1986 Melosira pseudoamericana Camburn

Meridion alansmithii Brant 2003
H:CAS:221016
I:CAS/ANSP: H.L. Smith 238
L:BM:25798 (H.L. Smith 237)
P:ANSP:51571
H:ANSP:44467
I:CAS/ANSP: T \& P (2) 36, 37
H:ANSP:4737a
H:ANSP:44466
I:CAS/ANSP:T \& P (2) 107, 108
I:CAS/ANSP: T \& P (2) 107, 108
L:ANSP:T \& P (2) 159
H:ANSP:44458
H:ANSP:44467
I:CAS/ANSP:T \& P (2) 107, 108
H:ANSP:44458
H:CAS:205078
I:CASSANSP: $\&$ P (2) 340, 341
H:ANSP:44489
H:Wiegand Herb., Cornell
H:ANSP:44492
H:ANSP:44489
H:ANSP:44484
H:ANSP:44474
さ
I:CAS/ANSP: T \& P (2) 103, I:CAS/ANSP: T \& P (2) 103, H:ANSP 44469
H:ANSP:44474
H:ANSP:44469
$\circ$
+
4
$\vdots$
4
4
4
H:CAS:205077
H:ANSP:44466
H:ANSP:44484
H:ANSP:45669
势

MA: Pelham
National Forest, Hoh River
MA: Pelham
WA: Olympic
TN: Knoxville
OH: Gambier
G. Gamier MD: Potomac River
CT: Birge's Pond
SC: Aiken Co.. Savannah River
MD: Potomac River
WA: Tacoma
NY: West Point
MA: Essex Co., Georgetown, Boldpatte Pond
PA: Ridley Creek
MD: Potomac River
WA: Tacoma
PA: Ridley Creek
OR
CT: Plainville, Hamlin's Pond
FL: Silver Springs
NY: Genesee Co., Bergen Swamp
SC: Aiken Co., Savannah River
FL: Silver Springs
FL: Silver Springs
FL: Silver Springs

[^5]Navicula bogotensis var. ininterrupta M. Peragallo in Tempère \&
Meridion anceps (Ehrenherg) Williams
Meridion hohiii Rhode 2001
Meridion anceps (Ehrenherg) Williams.
Meridion intermedium H.L. Smith 1878
Meridion lineare (H.L. Smith) D.M. Williams
Microsiphoma potamos Weber
Navicula achthera Hohn \& Hellerman 1963
Navicula acrosphaeria var: dilata Tempère \& Peragallo 1908
Nowicula aikenenses Patrick
Navicuta alea Hohn \& Hellerman 1963
Navicula alpina var. elongata M. Peragallo in
Tempère \& Peragallo 1908
Navicula americana Ehrenberg
Navicula americana var. moesta Tempère \& Peragallo Navicula ammicola I Iohn \& Itellerman 196.3

Navicula anatis: Hohn \& Hellerman 1963
Navicula antinitescens M. Peragallo in Temper
Navicula argutiola Hohn \& Hellerman 1963
Navicula aurora Sovereign Navicula bastanit M. Pergano in

Navicula baesma Honn-
Navicula betgenemsis Ho 1959
Navical bicome 1961
Navicula birhis Hohn 1961
Navicula bita Hohn 1961
H:CAS:205092
H:ANSP:4737a
H:ANSP:3954a
H:ANSP:44467
H:ANSP:6679a
H:ISU: Il-14-69 \#3
H:ANSP:Boyer A-6-15
H:ANSP:45669
I:CAS/ANSP: T \& P (2) 103, 104
H:ANSP:44487
H:ANSP:44496
H:ANSP:44468
I:CAS/ANSP: T \& P (2) 586-588
H:ANSP:8035
H:ANSP:4426a
H:ANSP:44254a
H:ANSP:44470
I:CAS/ANSP: T \& P (2)103, 104
L:ANSPT \& P (2) 104?
H:CAS:NY Elmore 704
H:ANSP:44491
H:CAS:205093
H:ANSP:2200
I:CAS/ANSP: 302,303
H:ANSP:53748
H:ANSP:45669
I:CAS/ANSP: T \& P (2) 365, 366
H:ANSP:42397a
H:ANSP:63245
H:ANSP:8031
H:BRM:N18/22
H:ANSP:44460
H:I.L.L.:L-6-46
H:ANSP:45669
H:ANSP:44470
H:ANSP:44491
H:ANSP:2197
H:CAS:205094
H:ANSP:44468
H:ANSP:44258a
H:ANSP:4072a
H:
WA: Pend Oreille Co., Bead Lake
SC: Aiken Co., Savannah River
SC: Aiken Co., Savannah River
MD: Potomac River
TX: Orange Co., Sabine River
IA
CO: Radford Peak
IN: Randolph Co., Cabin Creek bog
CT: Bristol, Fall Mountain
FL: Silver Springs
SC: Aiken Co., Savannah River
PA: Ridley Creek
ME: Crane Pond
TX: Orange Co., Sabine River
SC: Aiken Co., slough of Savannah River
SC: Aiken Co., near mouth of Upper Three Runs
PA: Ridley Creek
CT: Bristol, Fall Mountain
CT: Bristol, Fall Mountain
NE: pool, I mile W of Fremont
FL: Silver Springs
WA: Pend Oreille Co., Bead Lake
PA: Pike Co., Shohola Falls
WA: Puget Sound, Orca Island
SC: York Co., Long Branch Creek
IN: Randolph Co., Cabin Creek bog
OR: Klamath Co., Swan Lake
PA: Lancaster Co., Little Muddy Creek
MT
TX: Orange Co., Sabine River
FL: St. Petersburg, Pass-a-Grille
PA: Ridley Creek
IA: Dickinson Co., Excelsior Fen
IN: Randolph Co., Cabin Creek bog
PA: Ridley Creek
FL: Silver Springs
PA: Pike Co., Shohola Falls
OR: Crater Lake National Park, Vidae Fall
MD: Potomac River
SC: Aiken Co., slough of Savannah River
SC: Aiken Co., Upper Three Runs
In

| H:ANSP:44466 |
| :---: |
| H:CAS: NY, Ward B-36-16 |
| H:BRM:N5/57 |
| H:ANSP:44260a |
| I:CAS/ANSP: T \& P (2) 365, 366 |
| H:ANSP:44460 |
| I:CAS:NY Elmore 634 |
| H:ANSP:44469 |
| H:ANSP:61083 |
| L:ANSP:Boyer 747 |
| H:ANSP:44497 |
| H:ANSP:62310d |
| H:ANSP:44469 |
| H:ANSP:44489 |
| H:ANSP:3568a |
| H:ANSP:44489 |
| H:ANSP:44469 |
| H:ANSP:44467 |
| H:ANSP:4613b |
| H:ANSP:44458 |
| H:ANSP:4695a |
| L:BRM:N10/7 |
| H:BRM:N14/31 |
| H:ANSP:44484 |
| H:ANSP:6853a |
| H:ANSP:6535 |
| H:ANSP:8030 |
| H:ANSP:61083 |
| H:ANSP:44466 |
| H:ANSP:44489 |
| H:ANSP:44274a |
| H:ANSP:2188 |
| I:CAS/ANSP: T \& P (2) 107, 108 |
| L:ANSP:T \& P (2) 365 |

$H:$ ANSP:44474
H:ANSP:2188
H:ANSP:45669
$H: A N S P: 45669$
MD: Potomac River
SC: Aiken Co., Upper Three Runs Creek
OR: Columbia River OR: Klamath Co., Swan Lake PA: Ridley Creek
ND: Devil's Lake
IA: Dickinson Co., Cayler Prairie AL: Mobile Co., Mobile PA:Chester Co., Ridley Creek NY: Mohawk River MT: Flathead Lake
PA: Ridley Creek
FL: Silver Springs
SC: Barnwell Co., Savannah River
FL: Silver Springs
PA: Ridley Creek
MD: Potomac River
VA: Louisa Co., North Anna River
PA: Ridley Creek PA: Lancaster Co., Lititz Run OR: Columbia River OR: Columbia River
FL: Silver Springs TX: Calhoun Co., Mission Lake
TX: Orange Co., Sabine River TX: Orange Co., Sabine River IA: Dickinson Co., Cayler Prairie PA: Ridley Creek
FL: Silver Springs
SC: Aiken Co., Savannah River
PA: Pike Co., Greeley
PA: Pike Co., Greeley
OR: Klamath Co., Swan Lake
OR:Columbia River
FL: Silver Springs PA:Pike Co., Greeley
IN: Randolph Co., Ca

Navicula peregrina var. truncata M. Peragallo in Tempère \& Peragallo 1908 Navicula peticolasii M. Peragallo Navicula placenta Ehrenberg
Navicula orangiana Patrick 1959
Navicula orbiculata Patrick 1959
Navicula nemoris Hohn \& Hellerman 1963 Navicula nimbus Hohn \& Hellerman 1963 Navicula notha Wallace
Vavicula mugalis Hohn \& Hellerman 1963 Navicula obdurata Hohn \& Hellerman 1963 Navicula oblongiformis Hustedt 1934 Navicula obtuseprotracta Hustedt 1966 Navicula ocallii Hohn 1961
Navicula odiosa Wallace
Navicula paludosa f. rhomboidea Reimer 1970
Navicula parablis Hohn \& Hellerman 1963
Navicula parodia Hohn 1961
Navicula parablis Hohn \& Hellerman 1963
Navicula parodia Hohn 1961
Navicula paucivisitata Patrick 1959
Navicula pennsylvanica Patrick
Navicula poconoensis Patrick 1945
Navicula potzgeri Reimer 1961
Navicula potgeri var. quadripunctata Reimer
H:ANSP:44466
H:CAS:NY J Grant 16 Nov 1928
H:ANSP:4737a
H:CAS:205095
I:CAS/ANSP: T \& P (2) 78
H:ANSP:4373b
H:CAS:205096
H:ANSP:44469
H:ANSP:44458
H:ANSP:44472
H:ANSP:8030
H:ANSP:44470
H:ANSP:4737a
H:ANSP:6564a
H:ANSP:44254a
H:ANSP:6604a
H:ANSP:4425a
H:ANSP:44259a
H:ANSP:44474
I:CAS/ANSP: \& P (2) 103, 104
H:ANSP:44259a
L:BRM:N10/2
H:ANSP:62306a
H:ANSP:6587a
L:BRM:N8/80
H:ANSP:44469
H:ANSP:44458
H:ANSP:62304b
H:CAS:205079
H:ANSP:4628a
H:CAS:NY Ward D-4-21
H:ANSP:53747

H:ANSP:44285a
H:ANSP:44266c
H:ANSP:44266b
H:ANSP:Boyer 778
H:CAS:221031
H:A

Narticulu psechloreinhlurdtii Pattron Naviculu pupula var: linecure Tempè̀ Navicula radiosa var. parva Wallace Navicula radiosa var. subrostrata Cleve Naricula rainierensis Sovereign
Navicula recava Hohn \& Hellerman 1963 Navicula rivalis Hohn \& Hellerman 1963 Navicula rugula Hohn \& Hellerman 1963 Navicula sabiniana Patrick
Navicula sagitta Hohn \& Hellerman 1963
Navicula savamnahicma Patrick
Navicula schroeteri var. escambia Patrick Navicula secura Patrick
Navicula secreta var. apiculata Patrick
Navicula seminulum var. hustedtii Patrick
Navicula simula Patrick 1959
Navicula askalenastriata Hohn 1961 . Peragallo in Tempère \& Pergallo 1908
Navicula smithii var. dilatata M. Peragallo in Tempère \& Pergallo 1908 Navicula subfasciata Patrick 1959
Navicula subhexagona Hustedt 1934
Navicula swaniana Moghadam
Navicula texana Patrick
Navicula typografica Hustedt 1930
Navicula umbra Hohn \& Hellerman 1963
Navicula venerablis Hohn \& Hellerman 1963 Navicula vitabunda var. montana Moghadam Navicula walkeri Sovereign Navicula wallacei Reimer 1966 Navicula wardii Patrick 1959
Neidium affine (Ehrenberg) Pfitzer Neidium affine var. humerus Reimer Neidium apiculatum Reimer
Neidium apiculatum var. constrictum Reimer
Neidium bisulcatum var. subundulatum (Grunow) Reimer Neidium boyeri Reimer
Neidium cape-codii Siver \& Hamilton in Siver et al.

H:CAS:205090
H:ANSP:8301
H:ANSP:8299a
H:ANSP:53919 H:ANSP:Boyer W-6-23 H:ANSP:Schulze 367
H:ANSP:T \& P (2) 211

[^6]

SC: Aiken Co., Upper Three Runs Creek MA: Bridgewater

WA: Callam Co., Ozette Lake
WA: Adams Co... Finnel Lake
NY: West Point
Several, NY, CT, MA, ME IA: Dickinson Co., W. Lake Okoboji A: Dickinson Co., W. Lake Okoboji Great Smoky Mountains National Park

NY: Sullivan Co.. Monticello
NJ: Winslow, Blue Hole, Inskip River
ME: York Co. (?), Saco Pond
CT: Hartford Co., Bristol, Tamarack Swamp ME: Cherryfield

$$
\begin{aligned}
& \text { SC: York Co., Long Branch Creek } \\
& \text { FL: Silver Springs }
\end{aligned}
$$

$$
\begin{aligned}
& \text { FL: Silver Springs } \\
& \text { WA: Pend Oreille Co., Bead Lake }
\end{aligned}
$$

MD: Potomac River
PA: Ridley Creek
TX: Guadalupe Co. Guadalupe River
SX: Guadalupe Co. Guadalupe River OR: Diamond Lake
IA: Kossuth Co., Union Slough
WA: Mt. Rainier National Park, Lake Louise OR: Crater Lake OR: Crater Lake PA: Ridley Creek

$$
\begin{aligned}
& \text { OR } \\
& \text { CA: Mono Lake }
\end{aligned}
$$

CA: Mono Lake OR: Diamond Lake
SC: York Co., Long Branch Creek WA: Pend Oreille Co., Bead Lake MD: Potomac River NY: Lake Champlain
MD: Potomac River PA: Ridley Creek

Neidium floridanum Reimer
Neiditm Neidium hercynicum f. subrostratum Wallace Neidium hitchoockii (Ehrenberg) Cleve Neidium hitchcockii f. teres Sovereign Neidium tumescens (Grunow) Cleve Neidium inconstans Sovereign

Neidiumi iridis (Ehrenherg) Cleve
Neidium iridis var: (amphigomphus (Ehrenberg) A. Mayer Neidium kozolwi var. baicalensis f. robusta Stoermer 1963 Neidium kozlowi var. undulata Stoermer 1963 Neiditm ladogense var. densestriatum f. peribryum Neidium maximum (Cleve) Meister

Neidium rudimentarum Reimer
Neidium sacoense Reimer
Nitzschia abridia C'amburn 1978 Nitzschia asymbasia llohn 1961 Niteschia bella Sovercign

Nitzschia biacrula Hohn \& Hellerman 1963
Nitzschia bicrena Hohn \& Hellerman 1963
Nitzschia bita Hohn \& Heilerman 1963
Nitzschia bulnheimiana var. capitata Reimer 1966
Nitzschia columbiana Sovereign 1958
Nitzschia congolensis var. mooreae Reimer 1982 Nitzschia dissipata f. undulata Sovereign Nitzschia exilis Sovereign 1958 Nitzschia fonticoloides Sovereign Nitzschia incomptus Hohn \& Hellerman 1963 Nitzschia innominata Sovereign

Nitzschia monoensis Kociolek \& Herbst 1992 Nitzschia montanestris Camburn 1978 Nitzschia oregana Sovereign Nizschia perspicillata Camburn 1978 Nitzschia perspicua Sovereign Nitzschia pertica Hohn \& Hellerman 1963 Nitzschia plana var. americana Hustedt 1924 Nitzschia reimerii Kociolek \& Herbst 1992 Nitzschia semidesum Hohn \& Hellerman 1963 Nitzschia sentiformis Hohn \& Hellerman 1963
H:Lange-Bertalot, BIUFaM:Am-N 69
H:ANSP:44268a $\mathrm{H}:$ ANSP:44268a
$\mathrm{H}:$ CAS:205080
H:CAS:205080
H:ANSP:57568
H:ANSP:57569
I:ANSP: $\boldsymbol{T}$ \& $P(2) 365366$
L:ANSP:H.L. Smith 238

H:ANSP:Boyer V-5-5
H:ANSP:2189
I:BRM:P1/50
L:ANSP:Boyer V-5-2
H:1049A
H:ANSP:2225
H:CAS:205097
H:ANSP:44458
L:ANSP: T \& P (2) 106 L:BRM:P1/89
H:NW:2009
H:ANSP:61660a
H:BRM:P2/3
H:BRM:P4/5
H:BRM:P2/12
H:ANSP:57550
Icono:Ehrenberg
Icono:Ehrenberg 1854: Fig. 2/III, 1


Nitaschia voldamica Sovereign 1958

## Nupela carolina Potapova \& Clason 2003 <br> Nupela neglecta Ponader, Lowe \& Potapova 2003 <br> Opephora americana M. Peragallo <br> Opephora ansata Hohn \& Hellerman 1963

Peronia intermedium (H.L. Smith) Patrick Pinnularia abaujensis var: lacustris Camburn \& Charles 2000
Pinnularia abaujensis var. rostrata (Patrick) Patrick Pinnularia abaujensis var. rostrata (Patrick) Patrick Pinnularia acrosphaeria var. turgidula Grunow ex Cleve
Pinnularia alabamae Krammer 2000
Pinnularia amblys Hohn \& Hellerman 1963
Pinnularia biceps var. pusilla Camburn \& Charles 2000
Pinnularia bigibba Gaiser \& Johansen 2000
Pinnularia bihastata (A. Mann) Patrick
Pinnularia bogotensis var. undulata (Peragallo) Pinnularia boyeri Patrick
Pinnularia burki Patick
Pinnularia cardinaliculis Cleve
Pinnularia caudata (Boyer) Patrick
Pinnularia cherryfieldiana Krammer 2000
Pinnularia clevei Patrick 1945
Pinnularia convexa Sovereign
Pinnularia cumvibia Hohn \& Hellerman 1963
Pinnularia cuneicephala (Mann) Patrick
Pinnularia dactylus var. dariana (A. Schmidt) Cleve
Pinnularia divergens var. bacillaris (M. Peragallo) Mills
Pinnularia elongata Hustedt 1934 Pinnularia erratica var. fossitis Krammer - Caw 1997 Pinnularia ferroindulgentissima Czarnecki \& Cawley 1997 Pinnularia flexuosa Cleve
Pinnularia flexuosa var. gibbosa Hustedt 1934
Pinnularia formica (Ehrenberg) Patrick
Pinnularia fossilis Krammer 2000
Pinnularia gibba var. gibba Hustedt 1934 Sulivan 2000
Pinnularia gibba var. gibba Hustedt 1934
Pinnularia gibbiformis var. floralensis Dute
Pinnularia gibbiformis var. floralensis Dute \& Sullivan 2000
H:ANSP:44458
H:ANSP:57554
H:BRM:P2/90
L:ANSP:Boyer 426
H:CAS:205098
H:ANSP:57554
H:ANSP:57558

H:CAS:205099
H:CAS:206002
H:CAS:205100
H:CAS:206003
H:CAS:206004
H:IOK:804

H:ANSP:57546a
H:ANSP:57547a
H:NW:2009
H:BRM:P3/78
H:CAS:206001
H:ANSP:57548a
H:ANSP:57559
H:CAS:206005
H:BRM:P2/74
H:BRM:P3/98
H:ANSP:57557
H:NAU:P100
H:CAS:221011
H:CAS:221011
H:

MA: Waltham, Crane Pond; French Pond
NY: Herkimer Co.. Merriam Lake NY: West Point
NJ: Hammonton Pond
"Monticello"
WA: King Co., Shadow Lake
MA: "Andower" Boston
NY: Herkimer Co.. Merriam Lake
MN: Lake Co., Dunnigan Lake UT: Salt Lake
WA: Skamania Co., Lake Olallie
WA: King Co., Stevens Pass, boggy meadow
WA: Grant Co., Vantage (fossil)
WA: King Co., Stevens Pass, boggy meadow
WA: Grant Co., Vantage (fossil) WA: Skamania Co., Lake Olallie WA: Adams Co., Finnel Lake FL: Clermont NJ: Hammonton Pond
USA: Laconia
|MA|: Crane Pond
PA: Media, Swampy pools
SC: Barnwell Co., oxbow lake
SC: Aiken Co., shallow Carolina bay MA: Waltham
WA: Kittitas Co., Haney Meadow
MA: Waltham; Hudson River; SC: Berkeley Co., Lime Sink
WI: Luce Co., King County, Shadow Lake WA: King County, Shadow Lake
USA: French's Pond USA: French's Pond
AL: Montgomery
OR: Columbia Rive
NY: Herkimer Co., Merriam Lake
AZ: Navajo Co., Cholla Lake
NM: Harding Co., Payton Lake
NM: Harding Co., Payton Lake

Plagiotropis arizonica Czarnecki \& Blinn 1978
Playaensis circumfimbriata Spaulding \& Kociolek 2002
Playaensis furtiva Spaulding \& Kociolek 2002
L:ANSP:Boyer M-7-19
H:ANSP: 103590 a
H:ANSP:4198
H:ANSP:4198
H:ANSP:103605b
H:ANSP:106157a
I:CAS/ANSP:H.L. Smith 447
H:ANSP:44254a
I:CAS/ANSP: T \& P (2) 103, 104
H:ANSP:57544a
H:I.L.L.:SP7
H:ANSP:8193
H:ANSP:Boyer V-V-3
H:ANSP:44272a
H:ANSP:H.L. Smith 502
S:ANSP:Febiger 4466, GC45953,
H.L. Smith F-56
$\mathrm{H}:$ ANSP:57564
H:ANSP: 106584 a
H:CAS:206012
H:ANSP:55143a

FL: DeLeon Spring

FL: Caloosahatchee River
CT: Avery Pond

CT: Avery Pond
CT: Avery Pond


## NE: Thomas Co., Dismal River

OH: Lake Erie at Cleveland NY: Niagara River at Buffalo

## OR: Pitt River

## FL: Caloosahatchee River

## CT: Bristol, Fall Mountain

AL: Montgomery

CT: Bristol, Fall Mountain CT: Bristol, Fall Mountain
SC: Aiken Co., shallow Carolina bay IA: Dickinson Co., Excelsior Fen AK: Nunivak Lake, Barrow, pool PA: Delaware Co., Newtown Square SC: Aiken Co., Upper Three Runs Creek MA: Suffolk Co., West Roxbury, near Boston NH: Carroll County, Wolfboro
NH: Exact locality not known
 CA: Merced Co., Merced River NH

WA: Skamania Co., Lake Olallie
Lake Michigan


Surirella terri Wind
Synedra cyclopum var. robustum Schulz. Synedra homostriata Hohn 1961
Synedra incisa Boyer
Synedra longiceps Ihrenberg I845 Synedra mazamaensis Sovereign Synedra recava Hohn 1961
Synedra socia Wallace
Synedra ulna var. chaseana Thomas

# A Widespread New Species in the Neotropical Berry-fruited Genus Clidemia and Range Extension of Ossaea quadrisulca (Melastomataceae: Miconieae) 

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#### Abstract

Clidemia almedae, a new species from Costa Rica, Panama, Colombia and Ecuador is described. The new species is closest morphologically to $C$. discolor from which it differs in the following characters: larger shrub or small tree with eciliate, larger leaves, long-pedunculate, bracteate inflorescences with sessile flowers congested in dense glomerules and subtended by ovate bracteoles, and larger berries. Diagnostic illustrations and color photographs of C. almedae at the type locality are included. The distributional range of Ossaea quadrisulca is extended to Mesoamerica on the basis of collections from Costa Rica.


#### Abstract

Resumen Clidemia almedae, una nueva especie de Costa Rica, Panamá, Colombia y Ecuador es descrita. La nueva especie es morfológicamente más cercana a $C$. discolor de la cual difiere en las siguentes características: arbusto más grande o árbol pequeño, hojas eciliadas más grandes, inflorescencias largo-pedunculadas, bracteadas, con flores sésiles en glomérulos densos y subtendidas por bracteolas ovadas, y bayas más grandes. Se incluyen ilustraciones diagnósticas, así como fotografías a color de $C$. almedae en la localidad tipo. El rango de distribución de Ossaea quadrisulca es extendido a Mesoamérica en base a colecciones de Costa Rica.


The Miconieae is the most diverse tribe of Melastomataceae with 30 genera and over 2200 species (Michelangeli et. al. 2004). Radiation in the tribe appears to be related to the presence of berry fruits, which have been favored by birds as dispersal agents. The second largest genus in the Miconieae after the "mega" diverse Miconia is Clidemia with over 180 species. Clidemia is separated from Miconia only by its lateral to pseudolateral inflorescences (Almeda 2004). Cogniaux (1888) separated Clidemia into five sections, but the characters used are highly suspect in defining monophyletic groups (Almeda 2004). For further detail on the circumscription of Clidemia see Almeda (2004).

In connection with field work conducted for the Manual of the Flora of Costa Rica project, botanists visited previously little-explored localities on the northern Caribbean slope of the Talamanca mountain range. Work in this region resulted in the discovery of one new species and one new distributional record of Melastomataceae for Costa Rica.

The new species of Clidemia described below was found at El Copal Wildlife Refuge, also in Pejibaye, Cartago, and is, in fact, widely distributed in southern Central America and northern South America.

## Clidemia almedae Kriebel, sp. nov.

Figures 1-2.
Type.- Costa Rica: Cartago: Cantón de Jiménez, Pejibaye, Selva, Reserva Biológica El Copal, $9^{\circ} 47^{\prime} \mathrm{N}, 83^{\circ} 45^{\prime} \mathrm{W}$, elev. $900-1080 \mathrm{~m}, 5$ July 2005, (fl, fr), R. Kriebel \& P. Ortiz 5106 (Holotype: INB!; isotypes: CR!).

Ramuli teretes sicut foliorum inflorescentia hypanthiaque glabri vel inconspicuo asperis induti. Petioli (2.5-) 4-12.7 cm longus; lamina (11-)18-32×(8.5-)14-23.5 cm ovata vel rotundata apice acuminata basi cordata vel rotundata, 7-9-nervata vel 7-9-plinervata. Inflorescentia lateralis $2-5.4 \mathrm{~cm}$ longa multiflora; flores 4 -meri, bractis et bracteolis $2-4 \times 1-2.5 \mathrm{~mm}$. Calycis tubus 0.75 mm longus, lobis interioribus $1-1.25 \times 1-1.25 \mathrm{~mm}$ ovatis, dentibus exterioribus $2-2.5 \times 2 \mathrm{~mm}$ ovatis. Stamina isomorphica glabra, antherarum thecae $1.25 \times 0.5 \mathrm{~mm}$ oblongis poro truncato vel dorsaliter inclinato; connectivum nec prolongatum nec appendiculatum. Ovarium 3-4-loculare et omnino inferum glabrum

Shrubs 1-4 m tall. Internodes rounded-quadrate; branchlets, petioles and elevated primary leaf veins below inconspicuously farinose-furfuraceous with minute hairs mostly less than 0.1 mm long. Leaves of a pair $\pm$ equal to unequal in size; petioles (2.5-) $4-12.7 \mathrm{~cm}$ long; blades (11-) 18-32× (8.5) 14-23.5 cm, ovate to rounded, apex acuminate, base cordate to subcordate, margin obscurely serrulate to serrulate-crenulate and ciliolate, 7-9-nerved or plinerved, innermost pair of primary veins arising ca. 1 cm above the blade base, adaxial surface glabrous or sometimes minutely pubescent on the primary veins towards the blade base, abaxial foliar surface inconspicuously farinosefurfuraceous on primary, secondary and higher order veins, otherwise glabrous. Inflorescence 2-5.4 cm long, an axillary cyme branched at the base into (1-)2-4(-6) bracteate, stout peduncles ca. 1.5-5 cm long terminating in aggregated glomerules of sessile flowers, often borne on defoliated nodes, peduncle divided nearly half way or towards the distal half of its length by two opposing and early deciduous bracts; bracts and bracteoles $2-4 \times 1-2.5 \mathrm{~mm}$, oblong to ovate. Flowers 4 -merous, sessile, each subtended by 2-3 bracteoles. Hypanthia (at anthesis) suburceolate with a cylindrical distal neck 1 mm long, glabrous. Calyx tube 0.75 mm long, calyx lobes $1-1.25 \times 1-1.25 \mathrm{~mm}$, ovatetriangular, fleshy, erect and totally concealed by the calyx teeth; calyx teeth $2-2.5 \times 2 \mathrm{~mm}$, broadly ovate, mucronate, fleshy, glabrous, widely spreading at anthesis and in fruit. Petals $2 \times 1.25 \mathrm{~mm}$, glabrous, translucent-white, oblong. Stamens isomorphic; filaments 2.25 mm long, glabrous, white; anthers $1.25 \times 0.5 \mathrm{~mm}$, white, turning brown with age. oblong, with a truncate to somewhat dorsally inclined apical pore, deeply channeled ventrally between the two anther cells; connective somewhat thickened dorsally but neither prolonged nor appendaged below the thecae. Ovary 3-4-locular, completely inferior, apex glabrous and smooth. Style $5-6 \mathrm{~mm}$ long, glabrous, erect to minutely declined at anthesis: stigma punctiform. Berry $5 \times 5-6 \mathrm{~mm}$, dark purple. Seeds 0.4 mm long, beige, ovoid to obovoid with a vaguely rugulose testa.

Phenology. - Specimens with flowers and fruits have been collected from May through November.

Distribution.- Known from rain forest and cloud forest in Costa Rica, Panama, Colombia and Ecuador at elevations from (480-)700-1100 m.

Paratypes.- Costa Rica: Cartago: Cantón de Jiménez, Pejibaye, Selva, Reserva Biológica El Copal. $9^{\circ} 47^{\prime}$ N. $83^{\circ}+5^{\prime} \mathrm{W} .30$ Jan. 2003. Kriebel \& Solano 2491 (CR, INB, MO); Cantón de Jiménez, Pejibaye, Selva, Reserva Biológica El Copal, sendero EL Ron Ron, $9^{\circ} 47^{\prime} \mathrm{N} .83^{\circ} 45^{\prime} \mathrm{W}, 28$ May 2005, Solano et. al. 2432 (CR. INB): Cantón de Turrialba, Parque Nacional Barbilla. sendero Topoyiyo, $9^{\circ} 58^{\prime} \mathrm{N}, 83^{\circ} 27^{\prime} \mathrm{W}$, Mora \& Rojas 1481 (CR. INB): Cantón de Turrialba. Javillo. $9^{\circ} 58^{\prime} \mathrm{N} .83^{\circ} 27^{\prime} \mathrm{W} .30$ Nov. 1994, Umaña et. al. 636 (CAS, CR); 13.6 km NE of Turrialba on road to Siquirres. 16 July 1976, Utley \& Utley 5435 (CAS). Heredia: Parque Nacional Braulio Carrillo. sendero La Botella, $10^{\circ} 09^{\prime}$ N. $83^{\circ} 57^{\prime}$ W, 11 Feb. 1993, Morales et. al. 1096 (INB).



#### Abstract

Limón: Cantón de Pococí, Parque Nacional Braulio Carrillo, Estación Quebrada Gonzáles a Salsipuedes, $10^{\circ} 09^{\prime} \mathrm{N}, 83^{\circ} 56^{\prime} \mathrm{W}, 11 \mathrm{Feb}$. 1993, Hammel et. al. 18817 (INB); Cantón de Siquirres, Altos Pascua, Quebrada Linda, $10^{\circ} 01^{\prime} \mathrm{N}, 83^{\circ} 38^{\prime} \mathrm{W}, 1$ Apr. 2001, Morales 7824 (INB). Panama: Veraguas: Vicinity of Santa Fé, along dirt road from Santa Fé to Río San Luis, past Escuela Alto de Piedra, at Río Segundo Brazo ( $2^{\text {nd }}$ stream below school on Atlantic Coast), $8^{\circ} 33^{\prime} \mathrm{N}, 81^{\circ} 08^{\prime} \mathrm{W}, 28$ June 1987, Croat 66882 (CAS, MO); $2-5 \mathrm{~km}$ NW de Santa Fé por el camino a Río Calovébora, 26 Aug. 1984, Hernández et. al. 747 (CAS, MO); Road past Escuela Agrícola Alto Piedra above Santa Fé to Continental Divide, Sytsma \& Andersson 4783 (CAS, MO). Columbia: Dpto. del Chocó: Municipio de San José del Palmar, hoya del Río Torito (afluente del Río Hábita), declive occidental, Finca "Los Guaduales", 1 Mar. 1980, Forero et. al. 6278 (CAS). Ecuador: Pichincha: Cantón de Quito, Parroquia Puerto Quito, Reserva Forestal de ENDESA, 10 km al norte de Alvaro Pérez Intriago, 11 June 1990, Cerón \& Ayala 10101 (CAS, MO, QCNE); Road Pedro Vicente Maldonado-El Cisne-La Celica, km 10 from Pedro Vicente Maldonado, $79^{\circ} 03^{\prime} \mathrm{N}, 00^{\circ} 08^{\prime} \mathrm{W}$, 15 Sept. 2001, Cotton et. al. 1720 (CAS, QCA); ca. 10 km from Santo Domingo de los Colorados, property of Tinlandia, 10 May 1980, Sobel \& Strudwick 2328 (CAS).


Discussion.- Clidemia almedae belongs in a species complex that includes C. discolor (Triana) Cogn., C. ostrina Gleason, C. crotonifolia Pilger, C. cordata Cogn., and C. urticoides Pilger. These species share a furfuraceous indument; leaves which tend to have rounded to cordate bases; truly axillary inflorescences often borne on defoliated nodes; 4-merous flowers; well-developed calyx teeth that often obscure the true calyx lobes; simple anther connectives; a completely inferior ovary; and smooth, granulate, asperulate, or vaguely rugulose, small seeds. Specimens in this complex tend to dry red, especially if treated with alcohol, and are a good source of red dye (pers. obs.). Except for C. almedae, all of the species mentioned above share a similar inflorescence architecture of laxly branched cymes with pedicellate flowers (but see below for comments on $C$. urticoides). Wurdack (1976) noted that the sizes of the inflorescences in C. discolor and C. ostrina are too variable to be of taxonomic utility. His assessment applies to the other members of this species group. The inflorescence of $C$. almedae differs from other members of this species complex by the presence of common bracteate peduncles and sessile flowers in congested glomerules that are subtended by two to three ovate bracteoles.

Wurdack (1976) believed C. crotonifolia and C. cordata were probably synonyms of C. discolor, but he evidently did not study the types. He also cited recent Peruvian collections from San Martín and Amazonas that were referable to C. discolor. Although it remains unclear whether these two species are synonymous with C. discolor, they are different from C. almedae in their laxly branched inflorescences. I thought the most similar species to C. almedae was Clidemia urticoides, that is until I examined the specimen Killip \& Smith 26340 (US), which had been cited by J.F. Macbride (1941) under this species for the Flora of Peru. Macbride noted that the specimens cited by him, which include the type Ule 6204, had been annotated as C. cordata by the late Henry Gleason but Macbride thought the inflorescences were different. The specimen Killip \& Smith 26340 (US) has five inflorescences with no flowers or fruits; it differs from typical C. discolor in the reduced inflorescences, but it is evident that the inflorescences lack common, bracteate peduncles. The branching in the inflorescences in Killip \& Smith 26340 suggests that C. urticoides falls within the range of variation exhibited in the inflorescences of $C$. discolor. Furthermore, $C$. urticoides has smaller leaves with ciliate margins like those of $C$. discolor. The type and other collections of $C$. urticoides are from Peru. the only country from which it is known. Although Clidemia discolor is also known from Peru, C. almedae is not, further suggesting the relationship of C. discolor and C. urticoides but not of C. almedae, which is known from Costa Rica, Panama, Colombia and Ecuador. It is possible that this complex includes only three "good" species: C. almedae, C. discolor, and C. ostrina, and that C. crotonifolia. C. cordata, and C. urticoides are synonyms of C. discolor.


FFr, ipe 2. Clidemia almedae. A. flower: B. fruit: C. and D. inflorescences. (From live material of Kriebel \& Orti: 5106)

Wurdack (1976) also noted the distinct congested inflorescence of what is here described as $C$. almedae and stated: "Throughout most of the range of the complex occasional collections show capitate-agglomerate inflorescences with variable 'peduncle' length; I believe these inflorescences are diseased or resulting from arthropod injury and that (ex char. and photo) C. urticoides will prove synonymous with $C$. discolor". Wurdack also questioned the specimens from Pichincha and Cotopaxi with long-pedunculate and bracteate inflorescences in the Flora of Ecuador. I have looked at live flowering and fruiting plants of both C. discolor and C. almedae in Costa Rica. Clidemia discolor is common in the Caribbean lowlands and south Pacific slope of the country; it is commonly a small shrub with ciliate leaves and laxly branched inflorescences. In those specimens with reduced inflorescences, the lax branching pattern is still evident and never resemble the inflorescences of $C$. almedae. Also, C. discolor tends to have smaller leaves and smaller fruit, which turn red and then purple, and subulate bracteoles. Clidemia almedae appears to have a patchy distribution, but it can be locally common. At the type locality, C. almedae is a common shrub or small tree that is dominant in secondary forests and forest margins. Although the length of the peduncle may vary, it is always present, the bracts are obvious, and the flowers, which are borne in dense clusters, are always sessile and subtended by ovate bracteoles. I have found no evidence of insect infestation or diseased inflorescences in a large population of C. almedae. Ovary locule number was counted in 35 dissected immature and mature fruits; 20 were 4 -locular and 15 were 3-locular. This variation is not exhibited in the constant 4-locular ovary of C. discolor. I have not found both species growing together, but it is possible that they do grow sympatrically in places like the Caribbean slope of the Central Cordillera of Costa Rica, in Braulio Carrillo National Park, where one of the paratypes of C. almedae was collected (Hammel 18817) and populations of C. discolor occur nearby (e.g., La Selva Biological Station, Heredia).

Other species related to this complex are C. epiphytica (Triana) Cogn., C. cursoris Wurdack, and C. rodrigue:ii Almeda, all of which have large leaves with a rounded to cordate base, axillary inflorescences commonly borne on defoliated nodes, 4-merous flowers, well developed calyx teeth, simple anther connectives, a completely inferior ovary and smooth, granulate, asperulate or vaguely rugulose small seeds. All of the above mentioned species differ from C. almedae in the structure of the inflorescence. Clidemia epiphytica also differs in its anisophyllous leaves and scandent habit, whereas C. cursoris and C. rodriguezii differ, among other things, in their consipuously quadrate to carinate stems.

Etymology.- It is with great pleasure that I name this species for Dr. Frank Almeda (CAS), who has studied the Melastomataceae for more than 30 years and recently finished an account of this greatly diverse family of flowering plants for the Flora Mesoamericana. I would also like to thank Dr. Almeda for donating most of his personal literature collection to the Botany Department at INB, which has been and continued to be of inestimatible help in our ongoing studies of the flora of Costa Rican.

## Comment on a new record for Ossaea quadrisulca (Naudin) Wurdack

Ossaea quadrisulca (Naudin) Wurdack (R. Kriebel 3913, CAS, CR INB, MO) from the La Marta Wildlife Refuge, Pejibaye, Cartago, was previously known from Colombia, Ecuador, Peru and Bolivia; this constitutes a confirmed new record for the Costa Rican flora. The specimens cited above are not the first known from Costa Rica; Wurdack (1973) cited Schnell 658 from Valle Escondido. Cartago, as perhaps belonging to this species, but he noted differences in pubescence and floral merosity. After studying pickled flowering material from Costa Rica and comparing it to specimens of South America, it is clear both belong to the same entity.

## Acknowledgments

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## Literature cited

Almeda, F. 2004. Novelties and nomenclatural adjustments in the Neotropical genus Clidemia (Melastomataceae: Miconieae). Proceedings of the California Academy of Sciences, ser. 4, 55(4):89-124.
Cogntaux, A. 1888. Melastomataceae (Clidemia). In C.F. P. von Martius, Flora Brasiliensis 14(4):468-511.
Macbride, J.F. 1941. Melastomataceae in Flora of Peru. Field Museum of Natural History, Botanical Series 13(4/1):249-521.
Michelangeli, F.A., D.S. Penneys, J. Giza, D. Soltis, M.H. Hils, and J.D. Skean Jr. 2004. A preliminary phylogeny of the tribe Miconieae (Melastomataceae) based on nrITS sequence data and its implications on inflorescence position. Taxon 53(2):279-290.
Wurdack, J.J. 1973. Certamen Melastomataceis XXII. Phytologia 26(6):397-408.
Wurdack, J.J. 1976. Certamen Melastomataceis XXV. Phytologia 35(1):1-13.
Wurdack, J.J. 1980. Melastomataceae. In G. Harling and B. Sparre, eds., Flora of Ecuador 13:1-406.

# A Revision of the Pachydactylus serval and P. weberi Groups (Reptilia: Gekkota: Gekkonidae) of Southern Africa, with the Description of Eight New Species 

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The Pachydactylus serval and weberi groups constitute a clade of small to moderate sized (typically $40-50 \mathrm{~mm}$ SVL), mostly rupicolous geckos that are distributed widely in western South Africa and Namibia, with scattered populations in eastern Namibia and adjacent northwestern Botswana. The taxonomic status of many of the described members of these groups has long been unresolved, and numerous subtly divergent populations have been identified since the last revisionary work was undertaken. Examination of more than 1800 specimens referable to these species groups permits recognition of at least 21 species, clearly divisible into serval and weberi subclades. Within these clades, most species are highly morphologically conservative, although there are diagnostic differences in a number of characters, most notably juvenile color pattern. The species boundaries so revealed are supported by phylogenetic evidence from the cytochrome $b$ mitochondrial gene. The validity of the currently recognized species in the $P$. serval/weberi clade ( $P$. serval, $P$. weberi, $P$. fasciatus, $P$. tsodiloensis, $P$. waterbergensis) is confirmed, and the taxa P. purcelli, P. acuminatus, $P$. werneri are elevated from synonymy or subspecific rank to full species. Pachydactylus robertsi, recently removed from the synonymy of $P$. scutatus, and $P$. kobosensis are confirmed as valid members of the $P$. weberi group. Pachydactylus sansteynae, originally described as a subspecies of $P$. serval, is a valid species but is not a member of $P$. serval/weberi clade. Pachydactylus montanus is a senior subjective synonym of $P$. onscepensis and is raised from the synonymy of $P$. serval. A genetically diverse taxon, $P$. montanus may include more than one biological species. In addition, eight new species are described and the existence of two additional taxa, each currently known from limited material, is noted. The areas of greatest diversity for the clade as a whole are along the lower Orange River and in southern Namibia. Both the Richtersveld/ Hunsberg region in the west and the Karasberge in the east harbor at least five species in the $P$. serval/weberi clade. The evolutionary history of the group is probably associated with the fragmentation of rocky substrates and the historical isolation of some regions by changing paleopositions of the drainage of the Orange River. Distribution patterns of geckos in this clade are coincident with those of cordylids and scorpions and together, these groups - all of which have explicit hypotheses of relationships - provide a possible basis for a fine-scaled biogeographic analysis of western portions of the southern African subcontinent.

Key words: Gekkonidae, Pachydactylus, systematics, species description, Namibia, South Africa, molecular phylogeny, biogeography

[^7]The monophyly of the southern African Pachydactylus group of geckos has long been recognized on the basis of the unique hyperphalangic condition of digit I of the manus and pes (Haacke 1968, 1976; Russell 1972; Joger 1985; Bauer 1990; Kluge and Nussbaum 1995). Monophyly of Pachydactylus itself, however, has been questioned on the grounds that: 1) it is made paraphyletic by its inclusion of the highly specialized taxa Colopus, Palmatogecko (including Kaokogecko) and Chondrodactylus, and 2) the precloacal pore-bearing P. tuberculosus and $P$. tetensis are basal to the remainder of Pachydactylus plus Rhoptropus (e.g., Joger 1985). The latter hypothesis has been rejected on the grounds of morphological, allozyme, and molecular evidence that supports Rhoptropus as the sister group of Pachydactylus sensu lato (Bauer and Good 1996; Lamb and Bauer 2001, 2002). The paraphyly of Pachydactylus relative to the burrowing genera Colopus, Palmatogecko, and Chondrodactylus was raised as a possibility by Haacke (1976) and explicitly proposed by Joger (1985). Bauer (1990) and Kluge and Nussbaum (1995) accepted Joger's interpretation as likely, but their own analyses were at the generic level and thus incapable of corroborating generic paraphyly. Recently, however, a phylogenetic analysis of the southern African Pachydactylus group based on mitochondrial and nuclear DNA sequence data (Bauer and Lamb 2005; Lamb and Bauer 2006) has confirmed Joger's (1985) hypothesis and demonstrated that each of the burrowing gecko genera evolved independently within Pachydactylus. Among the taxonomic consequences of this work has been the allocation of several species of Pachydactylus to the genera Elasmodactylus, Chondrodactylus and Colopus. Nonetheless, Pachydactylus remains the most speciose genus of southern African geckos.

Within Pachydactylus sensu stricto, a number of species groups have been recognized on the basis of overall morphological similarity (e.g., McLachlan and Spence 1966; Broadley 1977). Several of these groups have been reexamined using combinations of morphological, allozyme, and DNA sequence data, resulting in both the confirmation of the monophyly of these groups and in the recognition of additional species level taxa. In particular, the P. rugosus group, P. capensis group, $P$. scutatus group, and $P$. namaquensis group have been the subject of recent reviews and revisions (Branch et al. 1996; Lamb and Bauer 2000; Bauer and Lamb 2002; Bauer et al. 2002; Broadley 2003). The monophyly of all of these groups has been corroborated in two recent molecular phylogenies (Bauer and Lamb 2005; Lamb and Bauer 2006). In these, the most complete phylogenetic analyses to date, the Pachydactylus serval/weberi group (McLachlan and Spence 1966) was revealed to be the sister group of the $P$. capensis group.

The serval/weberi group has been among the most problematic components of Pachydactylus and, until now, species boundaries within this group have defied resolution. Members of the group are relatively small (typically $<50 \mathrm{~mm}$ SVL), primarily rock-dwelling geckos with relatively flattened bodies, distributed from the Western Cape Province of South Africa through northern Namibia. Despite being widespread and locally abundant, these geckos have had a long history of taxonomic confusion, stemming in part from the poor sampling that characterized most southern African geckos until the middle third of the $20^{\text {th }}$ century, when V. F. FitzSimons of the Transvaal Museum made important collections throughout much of the arid zones of southwestern Africa. At present only two species, $P$. weberi Roux, 1907 and $P$. serval Werner, 1910, are recognized by most authors (e.g., Branch 1998; Griffin 2003), and the non-nominate subspecies P. serval purcelli, P. s. onscepensis, P. weberi acuminatus, and $P$. w. werneri are sometimes regarded as valid (e.g., Kluge 2001). Pachydactylus sansteynae (formerly sansteyni, see Michels and Bauer 2004) was initially described as a subspecies of P. serval (Steyn and Mitchell 1967) but has long been recognized as specifically distinct (Branch 1988). Most recently, P. robertsi, formerly regarded as a subspecies of $P$. scutatus, has been demonstrated to be closely allied to the $P$. weberi complex (Bauer et al. 2002).

Historical Resumé of the P. serval and P. weberi Groups to 1943.- Prior to the major revisionary works of FitzSimons (1943) and Loveridge (1947), a great deal of taxonomic confusion existed with respect to various members of the $P$. serval and $P$. weberi groups and other small-bodied Pachydactylus (sensu Lamb and Bauer 2002). The first specimens referable to the weberi group were reported by Peters (1867), who identified two specimens (ZMB 5711) from Neu Barmen (now Gross Barmen, Namibia) as P. capensis. One of these was subsequently identified as P. formosus by Sternfeld (1911a) and was only much later (Loveridge 1947; Mertens 1955) correctly identified as $P$. fasciatus.

Roux (1907) described Pachydactylus weberi on the basis of four specimens (Fig. 1) from Klipfontein, Little Namaqualand. Based on comparisons with the few species then recognized in the genus, he considered the form to be intermediate between P. capensis and P. formosus. Werner (1910) recognized 17 species of Pachydactylus and described and illustrated $P$. serval from material from Farm Chamis, Great Namaqualand (Fig. 2). He considered the species to be closely allied to $P$. ocellatus $(=P$. geijte). Although he did not record $P$. weberi from the collection he described, his illustration of a juvenile P. fasciatus from Kammagas (Fig. 3; now MCZ R 21019) is, in fact, referable to this species.

Boulenger (1910) recognized 15 taxa of Pachydactylus in southern Africa. He described P. purcelli on the basis of material from Touwsrivier and Little Namaqualand. His key segregated $P$. weberi from P. serval and $P$. purcelli on the basis of tubercular vs. smooth dorsal scalation. The new species, P. purcelli, was characterized as having "rostral nearly twice as broad as deep, entering the nostril; snout a little longer than the orbit" as opposed to P. serval, which he described as "rostral but little broader than deep; snout much longer than the orbit."

Sternfeld (1911a) described P. pardus from Warmbad as a member of a group containing both P. serval and $P$. purcelli, separating his new form on the basis of the shape of the ear opening, length of the snout, width of the rostral, and size of the eye. Sternfeld (1911b) regarded $P$. weberi as a rare species closely allied to $P$. capensis and known to him only from Windhoek and Klipfontein. His view regarding the similarity of $P$. capensis and $P$. weberi stems in part from the fact that his specimens of "P. capensis" from Steinkopf were actually P. weberi. He considered P. serval to be rare, as it was still known only from the type material from Chamis.

Methuen and Hewitt (1914) recognized 18 species in Pachydactylus and added P. montanus from Lord Hill's Peak in the Great Karas Mountains to the serval/weberi group. These authors had not seen material of P. fasciatus, P. serval, or P. weberi. Nonetheless, they considered the new species related to $P$. weberi. They also provided a more extensive description and illustrations of $P$. purcelli (Fig. 4) and synonymized P. pardus with $P$. purcelli. Their key to the taxa, like that of Boulenger (1910), first grouped taxa by dorsal scalation. They distinguished $P$. purcelli from $P$. serval on the basis of the entry of the rostral into the nostril in the former only (in fact it enters in both forms). Pachydactylus montanus was distinguished from P. weberi by having the rostral and first labial entering the nostril (first labial but not rostral in $P$. weberi), the first labial being four-sided (pentagonal in $P$. weberi), and possessing 7 subdigital lamellae ( $5-6$ in $P$. weberi).

Werner (1915) reported on two specimens of P. weberi from Karibib and Keetmanshoop, Namibia. Both he and Hewitt (1910) noted the similarity of P. fasciatus and P. weberi, and the latter author even considered fasciatus, weberi and formosus as subspecific forms of $P$. capensis (Hewitt 1910, 1911, 1927).

Hewitt (1927) recognized 27 species and subspecies of Pachydactylus and subsequently described several members of the serval and weberi complexes. In describing $P$. capensis gariesensis, Hewitt (1932) expressed the belief that its affinities lay with $P$. weberi (also regarded by him as a subspecies of $P$. capensis), which he believed had a more northerly distribution. Hewitt had not
examined typical weberi, but did compare his material to a specimen from Karibib that he believed to be $P$. weberi (this specimen is, in fact, referable to P. fasciatus). Hewitt (1932) also noted similarities between gariesensis and affinis, the latter a true member of the capensis group (Broadley 1977; Bauer and Lamb 2002). Hewitt (1935) suggested that Werner's (1915) specimens of " $P$. weberi" from Keetmanshoop and Karibib may have been misidentified representatives of another new subspecies, P. c. werneri, described from the Khan River in west central Namibia. He also described P. montanus onscepensis, which he considered a probable relative of $P$. fasciatus, from the southern bank of the Orange River. He further maintained his earlier view that $P$. weberi was best regarded as a subspecies of capensis and that it was closely allied to his P. c. gariesensis.

Parker (1936) reported $P$. weberi from several farms near Windhoek. He reviewed Hewitt's $(1932,1935)$ comments on the group and regarded the evidence for the inclusion of $P$. weberi as a subspecies of $P$. capensis as weak. Parker (1936) also synonymized Hewitt's P. capensis werneri with $P$. weberi.

FitzSimons (1935) identified a specimen from Vredendal, in the Western Cape as P. fasciatus and recorded several new localities for $P$. purcelli in the northern Cape (Pofadder, Kakamas, near Kenhardt, and Onseepkans). FitzSimons (1938) subsequently reidentified the Vredendal specimen (TM 15797) as $P$. weberi gariesensis, but cited new material of $P$. fasciatus from the Hantamsberg, north of Calvinia (TM 18180, 18182-83). He also added new localities in Namaqualand for $P$. w. weberi and questionably assigned several specimens from Konkiep (TM 17722) and Aus (TM 17689-95) in southern Namibia to this form as well. FitzSimons (1938) identified material from southwestern Namibia and from Goodhouse as P. montanus onscepensis, but noted that the Namibian specimens might be referable to $P$. serval, then still known only from the types and Werner's (1910) terse description.

FitzSimons (1938) also described two additional species, P. kobosensis from the Rehoboth district of central Namibia, which he regarded as allied with P. capensis and "associated forms," and P. robertsi, a strongly keeled gecko from the Great Karas Mountains, which he interpreted as allied to $P$. scutatus. FitzSimons (1941) later reevaluated his Namibian "weberi" specimens and described them as $P$. weberi acuminatus. He suggested that Werner's (1915) record of $P$. weberi from Keetmanshoop was referable to this form and that "weberi" from Windhoek and Gobabis (Sternfeld 1911a) and Windhoek and Hoffnung (Parker 1936) probably represented yet another undescribed subspecies of $P$. weberi.

Pachydactylus serval and P. weberi since 1943.- FitzSimons (1943), in his Lizards of South Africa, reviewed the entire saurian fauna then known from the area now including South Africa, Namibia, Botswana, Swaziland, Lesotho, and Zimbabwe. In this work, which represents a transition to the "modern" era of lizard systematics in southern Africa, he recognized 40 species and subspecies of Pachydactylus. Among the taxa discussed above, he considered as valid the following: P. purcelli, P. serval, P. kobosensis, P. m. montanus, P. m. onscepensis, P. werneri, P. robertsi, P. fasciatus, P. w. weberi, P.w. gariesensis, and P. w. acuminatus. Thus, only P. pardus among the then existing names in the $P$. serval/weberi group was placed in synonymy.

Loveridge (1944) subsequently placed $P$. robertsi in the synonymy of $P$. scutatus as a valid subspecies. In his revision of African geckos, which represents an independent but essentially parallel revision of the same gekkonid taxa considered by FitzSimons (1943), Loveridge (1947) synonymized $P$. montanus and $P$. m. onscepensis with $P$. serval and regarded $P$. werneri as a subspecies of $P$. weberi.

Mertens (1955) recorded P. kobosensis, P. fasciatus, P. scutatus robertsi, P. purcelli, P. serval, $P$. weberi acuminatus and $P$. werneri from Namibia, following Loveridge's (1947) taxonomy except with respect to the last species. Wermuth (1965) recognized the same taxa as Mertens (1955) and
accepted Loveridge's (1947) usages for the forms restricted to South Africa.
The only subsequent concerted attempt to revise the serval/weberi group was that by McLachlan and Spence (1966), who reviewed some of the confusing taxonomic issues surrounding the group. They attempted to resolve the status of the several names then applied to different populations based on newly acquired collections made along the Orange River, where $P$. purcelli, $P$. serval, and $P$. montanus onscepensis were believed to occur in proximity. They considered dorsal color pattern to be uninformative and focused instead on dorsal tuberculation, identifying significant variation in this feature across the range of the serval complex as a whole. They found tuberculation to be absent in material from considerably south of the Orange River (typical purcelli), moderate in southern Namibian material (typical serval) and along the Orange River above Augrabies Falls, and generally strong in specimens from the South African side of the lower Orange Valley, increasing westward towards the Richtersveld (onscepensis). They interpreted these data as indicative of a single species composed of three subspecies.

Mertens (1971) accepted McLachlan and Spence's (1966) interpretation of the serval complex, but otherwise retained his earlier application of names. Branch (1981) recognized three forms as occurring in the then Cape Province. He followed McLachlan and Spence (1966) in regarding P. s. onscepensis and P. s. purcelli to be subspecifically distinct. Stuart (1980) and McLachlan (in Branch 1981) regarded werneri as a subspecies of $P$. weberi, and the latter regarded gariesensis as a synonym of $P$. w. weberi. Welch (1982) accepted some but not all of the previous synonymies, providing no justification for his actions (Table 1).

Visser (1984) recognized all three subspecies of $P$. serval but delineated slightly different distribution patterns for these forms compared to McLachlan and Spence (1966). He considered P. s. serval as a northern form, extending southwards to about $27^{\circ} 30^{\prime} \mathrm{S}$ and from the edge of the Namib east to about $19^{\circ}$ E, P. s. purcelli as a southern form extending from the Little Karoo north to the Orange River and into south-central Namibia to about $27^{\circ} \mathrm{S}$, and $P$. s. onscepensis as a lower Orange River form ranging from Augrabies to the Richtersveld and extending northwards towards Aus and Bethanie. He recognized a single form of $P$. weberi, distributed more or less continuously through Namaqualand, then discontinuously through Namibia, as far as $19^{\circ} \mathrm{S}$.

Branch (1988, 1994a, 1998) did not recognize subspecies within $P$. weberi but did accept P.s. onscepensis and $P$. s. purcelli as subspecifically valid. Neither did he recognize $P$. kobosensis, which McLachlan considered as a synonym of $P$. weberi (fide Griffin 2003). Not all authors have followed Branch's use of names (e.g., Rösler 2000; Kluge 2001; Griffin 2003 - all of whom recognized as valid several additional taxa); however, as the result of the wide use of Branch's Field Guide to the Snakes and Other Reptiles of Southern Africa, these names have gained wide acceptence among herpetologists in southern Africa. Most recently Bauer and Branch (2003) signaled the incompatability between the names in use for the $P$. serval group and the realities of variation observed in much larger samples than were available to McLachlan and Spence (1966).

Although most recent authors have not confused Pachydactylus fasciatus with $P$. weberi, as did some earlier authors, Haacke (1965) noted the similarity in scalation between the two, and the similar color pattern of the juveniles. Haacke (1966) in describing $P$. tsodiloensis regarded it as a member of the $P$. weberi group, distinguished from other members by its larger size, stockier build, enlarged posterior supralabials and distinctive color pattern. Bauer and Lamb (2003a) described an additional representative to the $P$. weberi group, $P$. waterbergensis, and presented molecular data confirming that $P$. fasciatus, $P$. tsodiloensis, and $P$. waterbergensis are each others closest relatives and members of a more inclusive clade that also includes the $P$. weberi and $P$. serval complexes.

Molecular phylogenetic analyses based on the mitochondrial genes cytochrome $b$ and 16 SrRNA supported the union of $P$. fasciatus and $P$. weberi as a clade outside of the $P$. capensis and
P. formosus groups (Lamb and Bauer 2000; Bauer and Lamb 2002) and nested well within a larger clade including the smaller-bodied species of Pachydactylus (Lamb and Bauer 2002). Most recently, mitochondrial data have been combined with data from the nuclear RAG-1 gene revealing that $P$. serval $+P$. weberi are the sister group of $P$. tsodiloensis $+P$. fasciatus and that this group as a whole is the sister group of the P. capensis group (Bauer and Lamb 2005; Lamb and Bauer 2006).

We here use a combination of morphological and molecular evidence to revise the remaining members of the Pachydactylus serval and $P$. weberi groups. Our objectives are to identify species boundaries within these complexes, to evaluate the validity of all previously described forms, to resolve phylogenetic relationships within the groups, and to interpret the evolution of these geckos in light of historical biogeography. Incomplete genetic sampling and a lack of material, especially juveniles (which generally exhibit diagnostic color patterns), from some regions, however, dictate that our taxonomic and phylogenetic conclusions, though robust, are not definitive, and more work remains to be done within this difficult group.

## Material and Methods

Specimens and Morphological Data.- The following measurements were taken with Brown and Sharpe Digit-cal Plus digital calipers (to the nearest 0.1 mm ): snout-vent length (SVL; from tip of snout to vent), trunk length (TrunkL; distance from axilla to groin measured from posterior edge of forelimb insertion to anterior edge of hindlimb insertion), head length (HeadL; distance between retroarticular process of jaw and snout-tip), head width (HeadW; maximum width of head), head height (HeadH; maximum height of head, from occiput to underside of jaws), snout to eye distance (SnEye; distance between anteriormost point of eye and tip of snout), nares to eye distance (NarEye; distance between anteriormost point of eye and nostril), orbital diameter (OrbD; greatest diameter of orbit), eye to ear distance (EyeEar; distance from anterior edge of ear opening to posterior corner of eye), ear length (EarL; longest dimension of ear), interorbital distance (Interorb; shortest distance between left and right supraciliary scale rows), forearm length (ForeaL; from base of palm to elbow), crus length (CrusL; from base of heel to knee), tail length (TailL; from vent to tip of tail), and tail width (TailW; measured at widest point of tail). Unless otherwise stated, counts and measurements were made on right side of specimens.

Scale counts and external observations of morphology were made using a Nikon SMZ-10 dissecting microscope. Preserved specimen photographs were taken with a Nikon CoolPix 990 digital camera. Radiographic observations were made using a Faxitron closed cabinet x-ray system. Museum symbolic codes follow Leviton et al. (1985), except for the National Museum of Namibia, Windhoek (formerly State Museum, Windhoek), for which we use the collection code employed by that institution (NMNW) in preference to SMW. Specimens for which molecular data were obtained are marked with an asterisk (*). Specimens were examined from the collections of Angelo J. Lambiris (AJL), Albany Museum (specimens now housed in Port Elizabeth Musuem, mostly recatalogued with PEM numbers (AM), Aaron M. Bauer (AMB), the American Museum of Natural History (AMNH), the California Academy of Sciences (CAS), Carnegie Museum of Natural History (CM), Field Museum of Natural History (FMNH), Institut Royal des Sciences Naturelles de Belgique (IRSNB), John D. Visser (JDV), Louisiana State University Museum of Natural Sciences (LSUMZ), Mirko Barts (MB), Museum of Comparative Zoology (MCZ), National Museum of Zimbabwe (former Umtali Museum collection [NMZB-UM]), Bayworld, Port Elizabeth Museum (PEM), South African Museum (SAM), Forschungsinstitut und Museum Senckenberg (SMF), National Museum of Namibia (SMW), Flagship Institution of the North,

Transvaal Museum (TM), University of Stellenbosch (USEC/H), Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Museum für Naturkunde, Berlin (ZMB), and Zoologisches Museum Hamburg (ZMH). Specimens from several of the personal collections referenced (AMB, MB) will be deposited in institutional collections or are currently awaiting registration numbers. In addition, original published descriptions and descriptions provided in broader faunal and taxonomic treatments (e.g., FitzSimons 1943; Loveridge 1947) have also been consulted.

Locality data have been taken from collection records. Latitude and longitude are generally given only when the collectors determined this themselves using a GPS or topographic map, or when an original locality was precise enough to warrant it. Regardless of the original form in which coordinates were recorded, we have presented them here in the form of degrees, minutes, seconds. For localities without precise coordinates we have determined quarter degree square references (QDS). The QDS system has been nearly universally used in large scale mapping of the southern African biota and remains a convenient approach to dealing with distributions. Under this system of notation, each single degree square is subdivided into four quarter degrees, designated A-D ( $\mathrm{A}=\mathrm{NW}$ quadrant, $\mathrm{B}=\mathrm{NE}$ quadrant, $\mathrm{C}=\mathrm{SW}$ quadrant, $\mathrm{D}=\mathrm{SE}$ quadrant). Each quarter degree is in turn divided into four similarly designated divisions, yielding a basic unit one sixteenth of a degree square, or one quarter of a degree on a side (e.g., 3015 Ac represents the unit bounded by $30^{\circ} 15^{\prime} \mathrm{S}$ and $30^{\circ} 30^{\prime} \mathrm{S}$ and $15^{\circ} 00^{\prime} \mathrm{E}$ and $15^{\circ} 15 \mathrm{E}$ ). All QDS references in this paper are to degrees South and East. Distances were assumed to be along recognized roads unless otherwise specified or implied by the original locality. Several possible quarter degree squares are listed in some cases where direction from a fixed point could be interpreted in several ways. Ambiguous localities are not plotted on the accompanying maps. Precise but doubtful localities are noted by question marks. In some cases district names were included in the original locality data. These have been reported as originally given, even in cases in which district boundaries have changed. However, we have allocated all localities for which some locality data exist to the currently recognized provincial (South Africa) or district (Namibia) units to which the localities now belong.

Molecular Data.- Tissue samples were processed at field collection sites and preserved in a saturated salt-DMSO buffer (Amos and Hoelzel 1991) or 95\% ethanol, or were initially preserved in liquid nitrogen and subsequently stored at $-80^{\circ} \mathrm{C}$. Genomic DNA was extracted from liver using the Qiagen QIAamp DNA Mini kit. Portions of the mitochondrial cytochrome $b$ (cytb) gene were used to assess sequence variation among specimens. The primers L14724 and H15149 (Meyer et al. 1990) were used to amplify a 400 bp segment of the cytb gene. Fifty ul reactions were amplified for 32 cycles at $92^{\circ} \mathrm{C}$ for $45 \mathrm{sec}, 55^{\circ} \mathrm{C}$ for 35 sec , and $72^{\circ} \mathrm{C}$ for 1 min . Amplification products were purified over Centri-sep columns and served as templates in cycle-sequencing reactions employing dye-labeled terminators (PRISM kit, Applied Biosystems, Inc.). PRISM reaction products were analyzed on an Applied Biosystems 373A automated DNA sequencer using dye-labeled terminators (BigDye ${ }^{\mathrm{TM}}$ Terminator kit, Applied Biosystems, Inc). Forward and reverse sequences were generated for each sample and their complementarity confirmed using the Sequence Navigator software (Applied Biosystems, Inc.). GenBank accession numbers for these sequences are presented in the Appendix. Sequences were aligned using the CLUSTAL X 1.81 program, applying default settings (Thompson et al. 1997). Pairwise sequence divergence estimates were derived using the Hasegawa-Kishino-Yano model (HKY85; Hasegawa et al. 1985), which assumes different evolutionary rates for transitions and transversions and unequal base frequencies.

Phylogenetic Analysis.- Our phylogenetic reconstruction is based on a partitioned Bayesian analysis. We used MrModeltest 2.0 (Nylander 2004) to identify appropriate models of sequence evolution for each codon position within cytb, based on the Akaike information criterion (AIC). We used MrBayes 3.0 b 4 (Huelsenbeck and Ronquist 2001) to conduct a Bayesian analysis,
incorporating three discrete substitution parameters corresponding to each codon position within $\mathrm{cyt} b$. The analysis was initiated with random starting trees and run for $1.0 \times 10^{6}$ generations, sampling trees every 100 generations. We used the Metropolis-coupled Markov chain Monte Carlo algorithm, engaging four incrementally heated Markov chains. To ensure Markov chains did not become entrapped on local optima, we analyzed the combined data in three separate runs. Burn-in was determined graphically; trees generated prior to burn-in (generally, the first 500 trees) were discarded. We used the MrBayes sumt command to create a majority rule consensus tree (all compat), generate an average likelihood score, calculate posterior clade probabilities ( pP ), and estimate average branch lengths across post burn-in trees. Pachydactylus affinis and P. capensis were used as outgroup taxa. Both are members of the $P$. capensis clade, the immediate sister group to the $P$. serval/weberi clade (Bauer and Lamb 2005).

## Systematics

Much of the confusion that characterized early work on the $P$. serval and $P$. weberi groups stems from the fact that virtually all members are morphologically conservative. Only $P$. fasciatus and $P$. tsodiloensis are readily distinguishable from all of their relatives because of their large size and somewhat more robust habitus. All remaining species are small to mid-sized Pachydactylus (< 50 mm SVL), exhibit a weakly to strongly depressed habitus, and are characterized by only a few major color pattern types. McLachlan and Spence (1966) regarded dorsal color pattern as an unreliable character but confirmed that several scale features had systematic value. In particular, they found that members of the weberi group were characterized by exclusion of the rostral from the nostril, whereas members of the serval group exhibited both rostral and first supralabial contribution to the nostril rim. Branch $(1988,1994 a, 1998)$ also used the presence of enlarged, keeled tubercles on the thighs to distinguish weberi group geckos from serval. McLachlan and Spence (1966) documented geographic variation in dorsal tuberculation among members of the $P$. serval group but their results suggested only trends, not clear cut diagnostic differences among the subspecific forms they recognized.

We examined more than 1800 specimens in these species complexes from throughout their ranges, under the assumption that such comprehensive sampling would reveal clearer patterns and more useful characters than had earlier studies. Unfortunately, we discovered that most traditional scale features used to distinguish closely related gecko species were either invariant across several putative taxa or varied extensively within taxa. We did, however, confirm the utility of the rostral scale character and found that color pattern was indeed useful in distinguishing taxa. In particular, we found that juvenile color pattern was stereotypical for each taxon, even if adult pattern was variable. The potential utility of juvenile pattern had been suggested by Haacke (1965) and Visser (1984), but has not previously been explicitly employed in a systematic context. We also found that dorsal tuberculation was useful in some instances and that taxonomically meaningful variation is evident with regard to the shape of the digits and relative size of scales on the snout and interorbital regions.

There has been much recent interest in species delimitation and its relationship to species concepts (Wiens and Servedio 2000; Wiens and Penkrot 2002; Ferguson 2002; Hebert et al. 2003; Sites and Marshall 2003, 2004; Blaxter 2004; Watson 2005). In this paper we follow a lineage-based species concept (Mayden 1997; de Queiroz 1998), but from a practical viewpoint, we are chiefly concerned with the properties such lineages express that permit us to infer species boundaries their diagnosability (Watson 2005). A variety of operational criteria for diagnosing species boundaries has been proposed (Sites and Marshall 2003, 2004). Wiens and Penkrot (2002) compared tree-
based approaches to species delimitation based on DNA data and both tree-based and characterbased approaches based on morphological data. Although numerous studies have found congruence between character- and mtDNA tree-based approaches with respect to species boundaries (e.g., Hollingsworth 1998), Wiens and Penkrot (2002) found signficiant discordance in their analysis of Sceloporus. In such cases they favored the species limits suggested by mtDNA data, arguing that some taxa exhibit high levels of within species phenotypic variation and relatively low between species differentiation and that such circumstances represented a "worst-case scenario" for morphologically based species delimitation. In these cases haplotype differentiation may occur more rapidly than diagnostic morphological characters, providing a more accurate picture of lineage boundaries.

The Pachydactylus serval/weberi group includes a large number of putative taxa that exhibit little intraspecific variation with respect to most morphological characters, but displays extensive intraspecific variation for some characters (McLachlan and Spence 1966). Ideally we would have preferred to have complete taxon sampling for our mtDNA data set. However, this was not feasible, given the remote areas in which some of these geckos occur and their often patchy distributions. Likewise we would prefer to have had adequate samples of each putative taxon to reliably assess whether the characters we have used are truly fixed (Wiens and Servedio 2000). Although our sample sizes were satisfactory for many of the taxa we examined, some species were represented by just one or only a few individuals. As a consequence we were unable to employ the method of Wiens and Penkrot (2002) explicitly - a circumstance we suspect would apply to systematic studies of many African squamates, which are typically poorly sampled. Instead we have analyzed the mtDNA data that was available and the character-based species delimitations in light of each other. Thus, in some cases, subtle differentiation revealed by scale counts was supported by strong support of monophyly in the gene tree, while in other cases, tree-based delimitations convinced us that perceived morphological character variation was of little taxonomic value. Although distribution patterns were not used to erect hypotheses of species boundaries, we considered geographic concordance with both the tree- and character-based species limits to be supportive of our taxonomic decisions (Brown and Diesmos 2001).

Our mtDNA data are employed chiefly in the context of species delimitation as described above, but we consider our hypotheses of relationships among species to be preliminary. Our mitochondrial data represent a single gene tree which, through retention of ancestral polymorphisms and/or incomplete lineage sorting, may not be congruent with the "true" species phylogeny of the group (Avise 1989; Moore 1995).

## Species in the Pachydactylus serval group

Based on morphological and molecular investigations, we recognize a total of 21 species in the $P$. serval/ weberi clade, making it by far the most speciose lineage in the genus. This includes the following previously described taxa: P. serval, P. purcelli, P. montanus, $P$. weberi, P. acuminatus, $P$. werneri, P. robertsi, P. fasciatus, P. tsodiloensis, P. waterbergensis, and $P$. kobosensis, as well as ten previously unnamed taxa. Eight of these are described herein, the two remaining will be described elsewhere. The members of the clade are chiefly rupicolous and share the following morphological features: body moderately to strongly depressed; nostril typically surrounded by supranasal, two postnasals, and first supralabial (except in P. kobosensis and rarely in other taxa); rostral variably excluded from nostril rim; 5-6 undivided adhesive lamellae beneath digit IV of pes (plus one terminal divided lamella); dorsal pattern of transverse bands or spots. All share the following skeletal features, which are plesiomorphic for Pachydactylus as a whole: phalangeal formula 3-3-4-5-4 for
manus and 3-3-4-5-4 for pes, 26 presacral vertebrae, a single pair of crescentic cloacal bones in males only. Below we provide new diagnoses for the previously named species and descriptions of the new taxa. Previously described taxa are presented in chronological order of original description. A partial phylogenetic analysis based on analysis of part of the cytochrome $b$ gene is presented following the the descriptions and diagnoses.

## Pachydactylus fasciatus Boulenger, 1888

Figures 5-9.
1867 Pachydactylus capensis Peters, Mber. Akad. Wiss. Berlin 1867:235.
1888 Pachydactylus fasciatus Boulenger, Ann. Mag. Nat. Hist. (6)2:138. (Lectotype [designated by Bauer and
Branch 1991]: BMNH 1946.8.25.99: "Namaqualand," don. L. Péringuey (see Bauer and Branch 1991 for a discussion of the type locality). Paralectotype: SAM 1052: same collection data as lectotype.)
1890 Pachydactylus fasciatus Boulenger, Proc. Zool. Soc. London 1890:78.
1898 Pachydactylus fasciatus Sclater, Ann. S. Afr. Mus. 1:103.
1910 P[achydactylus] fasciatus Boulenger, Ann. S. Afr. Mus. 5:461.
1910 Pachydactylus fasciatus Hewitt, Ann. Transvaal Mus. 2:79.
1911 Pachydactylus formosus Sternfeld, Mitt. Zool. Mus. Berlin 5:397.
1911 Pachydactylus fasciatus Sternfeld, Mitt. Zool. Mus. Berlin 5:397.
1911 Pachydactylus fasciatus [part] Sternfeld, Fauna dtsch. Kolon. 4(2):15.
1911 P[achydactylus]. fasciatus Hewitt, Ann. Transvaal Mus. 3:44.
1915 Pachydactylus weberi [part] Werner in Michaelsen, Land und Süsswasserfauna Deutsch-Südwest Afrikas
I:334 (see Bauer and Branch 1991).
1927 [Pachydactylus] fasciatus Hewitt, Rec. Albany Mus. 3:400.
1929 Pachydactylus fasciatus Lawrence, J. S.W. Afr. Sci. Soc. 2:25.
1935 [Pachydactylus] fasciatus Hewitt, Rec. Albany Mus. 4:318.
1943 Pachydactylus fasciatus FitzSimons, Mem. Transvaal Mus. 1:87, pl. IX, fig. 1.
1947 Pachydactylus weberi acuminatus [part] Loveridge, Bull. Mus. Comp. Zool. 98:393.
1947 Pachydactylus weberi werneri [part] Loveridge, Bull. Mus. Comp. Zool. 98:394.
1947 Pachydactylus fasciatus [part] Loveridge, Bull. Mus. Comp. Zool. 98:395.
1947 Pachydactylus bibronii turneri [part] Loveridge, Bull. Mus. Comp. Zool. 98:405.
1955 Pachydactylus fasciatus Mertens, Abhandl. Senckenberg. naturf. Ges. 490:45.
1965 Pachydactylus fasciatus Wermuth, Das Tierreich 80:118.
1971. Pachydactylus fasciatus Mertens, Abhandl. Senckenberg. naturf. Ges. 529:39.

1982 Pachydactylus fasciatus Welch, Herpetology of Africa: 34.
1988 Pachydactylus fasciatus Branch, Field Guide:202, pl. 86, upper middle right, lower middle right.
1991 [Pachydactylus] fasciatus Kluge, Smithson. Herpetol. Inform. Serv. 85:23.
1993 [Pachydactylus] fasciatus Kluge, Gekkonoid Lizard Taxonomy:24.
1993 Pachydactylus fasciatus Bauer et al., Madoqua 18 :126, fig. 8, color plate (p. 145), fig. 8.
1994 Pachydactylus fasciatus Welch, Lizards of the World 1:93.
1994 Pachydactylus fasciatus Branch, Field Guide, 2nd ed.:202, pl. 86, upper middle right, lower middle right. 1998 Pachydactylus fasciatus Branch. Field Guide, 3rd ed.:253, pl. 86, upper middle right, lower middle right. 2000 [Pachydactylus] fasciatus Rösler, Gekkota 2:98.
2001 [Pachydactylus] fasciatus Kluge, Hamadryad 26:20.
2003 Pachydactylus fasciatus Griffin, Namibian Reptiles:33.
2003 P[achydactylus]. fasciatus Bauer and Lamb, Cimbebasia 19:3.
2005 P[achydactylus]. fasciatus Bauer and Lamb, Afr. J. Herpetol. 54:116.
Material examined.- Namibla: Karasburg District: TM 79074, Warmbad ( $28^{\circ} 26^{\prime}$ S, $18^{\circ} 44^{\prime}$ E); Bethanie District: ZMB 23374, Kuibis (2616Db); Walvis Bay District: ZMB 44031, Walvis Bay (2214Cd) [almost certainly in error]; Karibib District: ZMB 5710-11, 23451-52, Neu Barmen (2216Ba); SAM 14495-96, Karibib (2115Dd); TM 36388, Farm Gross Spitzkoppe ( $21^{\circ} 50^{\prime} \mathrm{S}, 15^{\circ} 12^{\prime} \mathrm{E}$ ); CAS 206936*, 10 km

E Spitzkop turnoff. Hentiesbaai-Usakos ( $21^{\circ} 57^{\prime} 08^{\prime \prime} \mathrm{S}, 15^{\circ} 16^{\prime} 48^{\prime \prime} \mathrm{E}$ ); ZFMK 66580-82, zwischen Swakopmund und Windhoek; Omaruru District: SMW R 7214, Brandberg Camp 3 (2114Ba); ZFMK 58579, Uis (2114Bb); Khorixas District: AJL 3440, 28 km W Khorixas (2014Bc); CAS 214672-77, 48 km W Kamanjab ( $19^{\circ} 39^{\prime} 14^{\prime \prime} \mathrm{S}, 14^{\circ} 21^{\prime} 03^{\prime \prime} \mathrm{E}$ ); CAS 176280, 48.6 km W Farm Franken, Kamanjab (1914Cb); CAS 176147, 49.5 km W Kamanjab (1914Cb); CAS 176159-66, 54.3 km W Kamanjab (1914Cb); CAS 223929-31, 58 km W Kamanjab ( $19^{\circ} 39^{\prime} 29^{\prime \prime}$ S $14^{\circ} 21^{\prime} 10^{\prime \prime} \mathrm{E}$ ); CAS $193681^{*}$, 59.3 km W Kamanjab ( $19^{\circ} 39^{\prime} 06^{\prime \prime}$ S, $14^{\circ} 21^{\prime} 20^{\prime \prime} \mathrm{E}$ ); CAS 176286-89, TM 69251, 64.9 km W Farm Franken, Kamanjab (1914Cb); PEM R 5058, 55 km W Kamanjab (1914Cb); PEM R 6142, 55.3 km W Kamanjab (1914Cb); PEM R 5059, 64.5 km W Kamanjab (1914Cb); CAS 214690-92, 74.2 km W Kamanjab ( $19^{\circ} 45^{\prime} 40^{\prime \prime} \mathrm{S}, 14^{\circ} 17^{\prime} 03^{\prime \prime} \mathrm{E}$ ); CAS 176093-95, 100.6 km W Kamanjab (1914Cc); CAS 176109, 108.9 km W Kamanjab (1914Cc); TM 68547, Palmwag (1913Dd); Outjo District: TM 39916. Farm Hoas ( $19^{\circ} 55^{\prime}$ 'S, $14^{\circ} 46^{\prime}$ E); Opuwo District: NMNW R 187-188, TM 29667, Warmquelle (1913Bb); TM 29667-29673, 48839-52, 45854, Sesfontein (1913Ba); SMF 46595, Kaokoveld; Imprecise Locality: SAM 1052 (paralectotype), Namaqualand. Erroneous Locality: SAM 1155, Natal. No Locality: ZMB 58364-67. Additional literature record: Namibia: Khorixas District: 8 km west of Khorixas (Haagner 1991).

Diagnosis.- A large (to 56.0 mm SVL, PEM R 6142) member of the $P$. serval/weberi clade that may be distinguished from all other members of this group by the combination of the following characters: rostral and sometimes first supralabial excluded from nostril; supranasals separated or in narrow to moderate contact anteriorly; scales on snout domed to conical, those on interorbital and parietal regions much smaller, granular, intermixed with tubercles approximately same size as snout scales; entire dorsum covered with enlarged, strongly keeled tubercles, regularly arranged in 16 (most commonly) -18 rows; thighs tuberculate; toe pads moderately broadly expanded, digits relatively long, slender; typically 5 undivided lamellae beneath digit IV of pes; tail to $115 \%$ SVL or more, bearing whorls of sharply keeled tubercles, often abutting one another; adult pattern consisting of well-defined broad, dark-edged, light saddle-shaped bands alternating with darker interspaces (Figs. 5-6; see also color photos in M. Griffin 1998, fig. 2.75; Barts 2002, figs. 1-2, 6). The lighter bands are cream to pinkish or grayish and the darker interspaces orange to russet to midbrown, with dark brown edges separating the two; juvenile pattern as adults, but especially boldly contrasting bands usually cream to pale yellow and dark chocolate brown and often less obviously saddle-shaped than in adults (Figs. 7-9; see also Haacke 1965, plate 2; Bauer et al. 1993, fig. 8; Barts 2002, figs. $8-10$ ).

Distribution.- The majority of records derive from the Khorixas, Omaruru, and Karibib districts of Namibia (Bauer and Branch 1991; Barts 2002; Griffin 2003), chiefly in areas above 1000 m elevation and north of the Swakop River (Figs. 10-11). However, there is a single verified record from Warmbad in the Karas District (Bauer and Lamb 2003b; Fig. 9). A record from the Bethanie District (Kuibis) may be valid, but one from Walvis Bay almost certainly reflects a point of shipment rather than of collection (Bauer and Branch 1991) and an old record from Natal (Boulenger 1910) has been shown to reflect incorrect data (FitzSimons 1943). All localities lie in or along the more mesic edge of the Nama-Karoo Biome (Irish 1994). Griffin (2000a) listed P. fasciatus as occurring on the plains around the Brandberg. We did not examine material from the Brandberg, but it is likely that the species occurs throughout the Omaruru District in appropriate habitats. All records from the Republic of South Africa (e.g., Boulenger 1910; Loveridge 1947) are incorrect. This species appears to be a strict Namibian endemic, although it may yet be found on the south bank of the Orange River, east of Goodhouse. Haacke (1965) noted that specimens of this species from Sesfontein may have escaped from captivity in Windhoek, but no evidence of an introduced established population has since come to light.

Natural History.- In the Khorixas District, this species is usually found by day under calcrete stones (Fig. 12) on sandy soil in savanna dominated by mopane (Colophospermum mopane)
and Acacia spp. (Bauer and Branch 1991; Bauer et al. 1993), and at Sesfontein it was taken under stones as well (Haacke 1965). A specimen from near Spitzkop (CAS 206936) was taken from under the bark of a fallen Acacia (Bauer et al. 1999). Pachydactylus fasciatus is chiefly terrestrial; reports of it being truly rupicolous (FitzSimons 1943; Loveridge 1947) probably stem from confusion with $P$. weberi.

Two eggs found in the wild measured $11.3 \times 9.0$ and $11.5 \times 8.9 \mathrm{~mm}$, respectively and contained near-term embryos. Eggshell structure was described by Röll (2001). Eggs are laid beneath stones and are partly covered by sand. Mating probably occurs in summer with oviposition in JanuaryFebruary and hatching in autumn (Bauer and Branch 1991). Feeding and reproduction in captivity have been reported by Barts (2002) and Rösler (2005) summarized data on incubation time and temperature, as well as egg and hatchling sizes.

Conservation Status.- Pachydactylus fasciatus is not known to occur in any Namibian national parks, except perhaps Gross Barmen Hot Springs, although it is present in a number of community-based conservancies which may offer some measure of protection. Griffin (2003) considered it likely to be present in the Etosha National Park, West Coast Recreation Area and the Namib-Naukluft Park. Where it occurs P. fasciatus is locally abundant and we do not consider it under any immediate threat. However, this is one of few members of the group that are offered for sale in the herpetocultural trade. A web search in October 2003 revealed adult (presumably captivebred) specimens being sold for US $\$ 75$ each.

Remarks.- We concur with Mertens (1955) in finding no evidence that $P$. fasciatus possesses as many as $9-10$ subdigital lamellae under the fourth toe (contra Boulenger 1888; Loveridge 1947).

## Pachydactylus weberi Roux, 1907

Figures 1, 3, 13-20.
1870 Pachydactylus capensis Peters, Mber. Akad. Wiss. Berlin 1870:110.
1907 Pachydactylus weberi Roux, Zool. Jb. Abt. Syst. 25:408, pl. 14, figs. 4-5 (Lectoype: ZMA 11046 [designated by Daan and Hillenius 1966] (Fig. 1): "Klipfontein, Kl.-Namaqualand;" coll. M. Weber, September 1894. Paralectotypes: ZMA 11047-48: same collection data as lectoype. A fourth paralectotype also does or did exist, probably in the NHMB collection in Basel (Daan and Hillenius 1966; van Tuijl 1995), although this specimen was not noted by Kramer (1979)).
1910 Pachydactilus fasciatus Werner, Zool. Anthropolog. Ergebn. Forsch. west. zentr. Südafrika:311, fig. 8 (Fig. 3).
1910 P[achydactylus] weberi Boulenger, Ann. S. Afr. Mus. 461.
1910 Pachydactylus weberi Hewitt, Ann. Transvaal Mus. 2:80.
1911 Pachydactylus Weberi [part] Sternfeld, Fauna dtsch. Kolon. 4(2):14.
1911 Pachydactylus fasciatus [part] Sternfeld, Fauna dtsch. Kolon. 4(2):15.
1911 [Pachydactylus] weberi Hewitt, Ann. Transvaal Mus. 3:44.
1914 P[achydactylus]. weberi Methuen \& Hewitt, Ann. Transvaal Mus. 4:129.
1927 [Pachydactylus] weberi Hewitt, Rec. Albany Mus. 3:400.
1932 Pachydactylus capensis gariesensis Hewitt, Ann. Natal Mus. 7:124, pl. VI, figs. 8-9 (Syntypes: SAM
17953 (originally nine specimens) (Fig. 13): "Garies;" coll. B. Peers (see Remarks)).
1932 [Pachydactylus] capensis weberi Hewitt, Ann. Natal Mus. 7:124.
1935 Pachydactylus capensis fasciatus FitzSimons, Ann. Transvaal Mus. 15:528.
1935 Pachydactylus capensis gariesensis FitzSimons, Ann. Transvaal Mus. 15:528.
1936 Pachydactylus weberi [part] Parker, Novit. Zool. 40:130.
1936 Pachydactylus capensis gariesensis Lawrence, Parasitology 28:11.
1936 Pachydactylus capensis weberi Lawrence, Parasitology 28:38
1936 Pachydactylus capensis fasciatus Lawrence, Parasitology 28:38 (non P. fasciatus Boulenger, 1888)

1938 Pachydactylus fasciatus FitzSimons, Ann. Transvaal Mus. 19:170.<br>1938 Pachydactylus weberi gariesensis FitzSimons, Ann. Transvaal Mus. 19:179.<br>1938 Pachydactylus weberi weberi FitzSimons, Ann. Transvaal Mus. 19:180.<br>19411938 Pachydactylus weberi gariesensis FitzSimons, Ann. Transvaal Mus. 20:359.<br>1943 Pachydactylus weberi weberi FitzSimons, Mem. Transvaal Mus. 1:88, pl. IX, fig. 2, pl. XV, Fig. 5.<br>1943 Pachydactylus weberi gariesensis FitzSimons, Mem. Transvaal Mus. 1:90, pl. IX, fig. 3.<br>1947 Pachydactylus weberi gariesensis Loveridge, Bull. Mus. Comp. Zool. 98:390.<br>1947 Pachydactylus weberi weberi Loveridge, Bull. Mus. Comp. Zool. 98:391.<br>1947 Pachydactylus fasciatus [part] Loveridge, Bull. Mus. Comp. Zool. 98:395.<br>1951 P[achydactylus]. weberi Lawrence, Ann. Transvaal Mus. 21:452.<br>1965 Pachydactylus weberi weberi Wermuth, Das Tierreich 80:123.<br>1981 Pachydactylus weberi weberi Branch, Ann. Cape Prov. Mus. (Nat. Hist.) 13:145.<br>1982 Pachydactylus weberi weberi Welch, Herpetology of Africa:36.<br>1982 Pachydactylus weberi gariesensis Welch, Herpetology of Africa:36.<br>1984 Pachydactylus weberi [part] Visser, Landbouweekbl. 27 April 1984:53, fig. p. 51, bottom.<br>1988 Pachydactylus weberi [part] Branch, Field Guide:208.<br>1991 [Pachydactylus] weberi Kluge, Smithson. Herpetol. Inform. Serv. 85:24.<br>1993 [Pachydactylus] weberi Kluge, Gekkonoid Lizard Taxonomy:25.<br>1994 Pachydactylus weberi Welch, Lizards of the World 1:95.<br>1994 Pachydactylus weberi [part] Branch, Field Guide, 2nd ed.:208.<br>1998 Pachydactylus weberi [part] Branch, Field Guide, 3rd ed.:263.<br>2000 [Pachydactylus] weberi weberi Rösler, Gekkota 2:100.<br>2001 [Pachydactylus] weberi Kluge, Hamadryad 26:21.<br>2002 Pachydactylus weberi Bauer et al., Proc. California Acad. Sci. 53:25.<br>2003 Pachydactylus cf. weberi [part] Bauer and Branch, Herpetol. Nat. Hist. 8:134.<br>2003 P[achydactylus]. w[eberi]. weberi Bauer and Lamb, Cimbebasia 19:3.<br>2005 P[achydactylus]. weberi [part] Bauer and Lamb, Afr. J. Herpetol. 54:116.

Material examined. - South Africa: Western Cape Province: TM 35020-22, Farm Waaikop, Ceres District (3220Ac); PEM R 12809, other side of Pakhuispas (3218Bb); SAM 44114 (3 specimens), TM 19612, 34311, Pakhuis Pass (3219Aa); USEC/H-2784, Pakhuis Pass ( $32^{\circ} 08^{\prime}$ S, $19^{\circ} 02^{\prime}$ E); SAM 44370 , Algeria (3219Ac); JDV 2498, Algeria Forestry Station (3219Ac); USEC/H-3013, Zuurvlakte ( $32^{\circ} 58^{\prime} 08^{\prime \prime} \mathrm{S}$, $19^{\circ} 03^{\prime} 04 \mathrm{E}^{\prime \prime}$ ); USEC/H-5562, Varsfontein, Tanqua Karoo National Park ( $32^{\circ} 11^{\prime} 00^{\prime \prime} \mathrm{S}$, $19^{\circ} 48^{\prime} 44^{\prime \prime} \mathrm{E}$ ); USEC/H5589, Mount Ceder ( $32^{\circ} 38^{\prime} 38^{\prime \prime}$ S, $19^{\circ} 25^{\prime} 22^{\prime \prime}$ E); JDV 64778, 75678, Farm Boskloof, near Citrusdal (3219Ca?), TM 35027, Gannagas Pass, Roggeveld Escarpment (3220Aa); USEC/H-2178, Holrivier (3118Cb); JDV 2729, 7 km W Bitterfontein (3118Aa); AM 241, PEM R 14782, Van Rhynsdorp (3118Da); SAM 43592-93, TM 42380, N of Van Rhynsdorp (3118Da); PEM R12810-20, 23 mi . N Van Rhynsdorp (3118Bc); PEM R 14770-71, 14773-74, 147776-78, TM 33983, Nuwerus (3118Ab); AM 243 (7 specimens), (3118Ab); AM 244 (11 specimens), Nuwerus District; PEM R 14736-39, SAM 18156 ( 12 specimens), TM 33984, Bitterfontein (3118Ab); USEC/H-2780-83, Bitterfonein ( $31^{\circ} 02^{\prime}$ S, $18^{\circ} 15^{\prime} \mathrm{E}$ ); JDV 72378, 72578, 72678, 72778, 72878, 72978, 73078, 73178, 73278, 73378, 73478, 73578, 73678, 73778, just N and S Bitterfontein (3118Ab); JDV 78078, 78178, 78278, 80978, just S Bitterfontein (3118Ab); JDV 81278(2), 81378, 5 km N Bitterfontein (3118Ab); JDV 1130, a few km E of Nuwerus (3118Ab); JDV 2609-10, 30 km N Koekenaap (3118Ad); TM 15797, Vredendal (3118Da); USEC/H-413, Oudenwagen, Bulshoek ( $31^{\circ} 48^{\prime} 00^{\prime \prime} \mathrm{S}$, $18^{\circ} 54^{\prime} 58^{\prime \prime} \mathrm{E}$ ); USEC/H-428, Blinkvlei, Urionskraal District ( $31^{\circ} 44^{\prime} 16^{\prime \prime} \mathrm{S}, 18^{\circ} 55^{\prime} 33^{\prime \prime} \mathrm{E}$ ); CM $119270-72,16.6 \mathrm{~km}$ N Bitterfontein (3018Cc); JDV N18780, Bruintjieshoogte, 40 km S Garies (3018Cc); TM 35132-34, 2 mi N Kliprand (3018Da); ZMH R07637, 33 km SW Kliprand (3018Cd); JDV 1412-17, 33 km S Kliprand (3018Dc). Northern Cape Province: PEM R 12795-97, 12854, 35 mi . from Loeriesfontein on Calvinia Rd. (3119Bc); TM 35105, 19 mi NNE Nieuwoudtville ( $31^{\circ} 23^{\prime}$ S, $19^{\circ} 02^{\prime}$ E); PEM R 12861-62, Downes near Calvinia (3119Bd); TM 18180, 18183, Hantamsberg ( 3119 Bc or 3119Bd); TM 18182, Calvinia ( $31^{\circ} 28^{\prime} \mathrm{S}, 19^{\circ} 47^{\prime} \mathrm{E}$ ); TM $35060-62$, Farm Groottoring, Calvinia District (3119Bc); TM 35053-59, Farm Agterhantam, Calvinia District (3119Ba); ZFMK 18336-38, Die Bos (3119Dc); TM 65920-21, Bloukrans Pass ( $31^{\circ} 40^{\prime}$ S, $19^{\circ} 45^{\prime}$ E); PEM R 12821-22,

25 mi . N Bitterfontein on Garies Rd. (3018Cc); AM 242 ( 27 specimens), Garies to 3018Ac; CAS 199997*-98*, 6 km S Garies on Hwy. N7 (3018Ca); JDV 1132-34, Farm Langdam, 18 km E Bitterfontein (3018Cd); JDV 5393, 81078(2), 81178(2), 50 km N Bitterfontein (3018Ca); IRSNB 11822, MCZ R 41842 (formerly TM 13719), 46815-16 (formerly TM 18147, 18153), 31573-74 (paratypes of Pachydactylus capensis gariesensis), SAM 17953 ( 13 specimens), 18053 ( 9 specimens), 43586, TM 18144-46, 18148-52, 18154, 18156-60, 33985-89, Garies (3017Db); JDV 71778, 72078, 72178, 72278, 72478, 78778, 81378, 5 km N Garies (3017Db); JDV 47080, 47280, 47380, 47480, 47580, N22180, 20 km W Garies (3017Db); TM 34035-38, 4 mi N Garies (3017Db); JDV 2558-59, 20 km past Molsvlei, Bitterfontein District (3017Dd); JDV 2631-33, 30 km past Molsvlei towards cost (3017Dd); JDV 2605-06, 2609, between Molsvlei and coast (3017); TM 15949-50, Soebatsfontein (3017Ba); SAM 18197 ( 2 specimens), TM 70092-93, Farm Leliefontein ( $30^{\circ} 18^{\prime} \mathrm{S}, 18^{\circ} 05^{\prime}$ E); PEM R 14741, 14744, 14749, 14752-53, 14759, 14762-65, 14767-69, Garies-Kamiesberg (3018Ac); JDV 1386, 1390, 1519, MCZ R 163278, 57 km N Kliprand (3018Bb); JDV 1378, 8 km N Kliprand (3018Da); JDV N17480, 7 km S Kharkams (3017Bd); JDV 71978, 5 km S Kharkams (3017Bd); JDV 1418, 1458, 1463, 1465-74, 15378, 77678, 82078, MCZ R 163281, Kharkams, S Kamieskroon (3017Bd); JDV N18280, N18380, N18480, 5 km N Kharkams (3017Bd); TM 34039-42, 10 mi N Garies (3017Bd); TM 34043-44, 6 mi SW Kamieskroon (3017Bd); CAS 186368*, 186369-70, 186371*, 186372-73, JDV 15278, SAM 18144 (11 specimens), 44288, 44321, Kamieskroon (3017Bb); TM 35220, 35219, 12 mi N Kamieskroon (3017Bb); CAS 186378, Kamiesberg Pass, 3 km E Kamieskroon (3017Bb); TM 35212, Kamiesberg Pass (3017Bb); JDV N12180, N13380, N13480, Wallekraal (3017Bc); JDV 80978, 81778, 81878, 81978, 3-5 km N Kharkams (3017Bd); SAM 47707-10, Kotzesrus ( $30^{\circ} 46^{\prime} 59^{\prime \prime} \mathrm{S}$, $17^{\circ} 48^{\prime 2} 20^{\prime \prime} \mathrm{E}$ ); MCZ R 163279, Juliesberg, E Kamiesberg, Kamieskroon (3018Aa); TM 34045, 7 mi E Kamieskroon on road to Gamoep (3018Aa): TM 35193-200, 4 mi NW Leliefontein (3018Aa); JDV 1397-98, 15 km W Farm Gorap on rd to Kamieskroon (3018Aa); JDV 51280, N16780, N16880, N16980, N17080, N20180, 24 km E Kamieskroon (3018Aa); JDV 1400, 1402-05, 1419, 58 km W Kliprand-Gamoep-Kamieskroon intersection (3018Aa); JDV N15380, N15480, N15580, N15680, N15780, N15880(2), N15980, N16080, N16180, N16280, N20880, 54 km E Kamieskroon (3018Ab); MCZ R 163280, Farm Gorap, E Kamiesberg, Kamieskroon (3018Ac); TM 35188, Farm Wolfhok (3018Ac); JDV 1144, 1157-58, 1160, 1164-67, 1169-77, 22 km W Aalwynsfontein (3018Ad); JDV 1374-75, Farm Dirkmaatjie, intersection Kamieskroon-KalkrandGamoep rds. (3018Ad); TM 35153-56, 30 mi W Loeriesfontein (3019Cc); JDV 48080, 48180, 100 km N Wallekraal (2917Ca); ZMH $07638,38 \mathrm{~km}$ W Gamoep (2918Cc); TM 34266-68, Gamoep, 26 mi E Kamieskroon (29Cd); JDV 81478(2), 26 km E Port Nolloth (2917Ac); TM 18132-34, 8 km S Komaggas (2917Cd); MCZ R 21019, PEM R12786-93, TM 34176-78, ZMB 23125, Komaggas (2917Cd); JDV 66378, Kamieskroon-Springbok; TM 34179-80, 4 mi from Komaggas on road to Springbok (2917Da); TM 34181-83, 34278-85, Spektal Pass (2917Da): JDV 70478, 70578, 70678, 70778, 70878, 70978, 71078, 71178, 71278, $71378,77778,77878,77978$, past Komaggas turnoff on rd. to Kleinsee from Springbok (2917Da); TM 34184, Naries/Eselsfontein Pass, 13 mi W Springbok (2917Da); MCZ R 46814 (formerly TM 18117), PEM R 12808, TM 18107-08, 18110-16, 18118-19, 32 miles from Springbok on road to Kamaggas ( $29^{\circ} 44^{\prime} \mathrm{S}, 17^{\circ} 31^{\prime} \mathrm{E}$ ); CM 130301-02, 11 km ENE Springbok (2917Db); JDV 74178, 74278, 74378, 74478, 74578, 74678, 74778, $74878,74978,75078,81578(2), 81678(2)$, N40280, 10 km S Springbok (2917Db); TM 18061-65, between O'okiep and Springbok (2917Db); USEC/H-2785-86, Springbok District (2917Db); SAM 46921, Die Stasie, Messelpad (2917Dc); IRSNB 11823 (formerly TM 17915), MCZ R 46813 (formerly TM 17912), PEM R 12847-48, TM 17909-11, 17913-14, 17916-17, Klipfontein (2917Ba); CAS 206823-24, Brandberg, Farms Kourootje and Kap Vley, De Beers Consolidated Farms ( $29^{\circ} 49^{\prime} 52^{\prime \prime} \mathrm{S}$, $17^{\circ} 22^{\prime} 35^{\prime \prime} \mathrm{E}$ ); TM 65855-57, 65859, Sandhoogte, Farm Ezelsfontein 214 ( $29^{\circ} 41^{\prime}$ S, $17^{\circ} 45^{\prime}$ E); PEM R 12784-85, SAM 18538 ( 6 specimens), Kleinsee (2917Ca); CAS 206752-53, 206754*, 206755-60, Kleinsee, Nature Reserve ( $29^{\circ} 38^{\prime} 49^{\prime \prime}$ S, $17^{\circ} 05^{\prime} 02^{\prime \prime} \mathrm{E}$ ); SAM 47706, Ratelpoort ( $29^{\circ} 26^{\prime} 22^{\prime \prime} \mathrm{S}, 17^{\circ} 50^{\prime} 00^{\prime} \mathrm{E}$ ); CAS 193318-30, 206902-04, LSUMZ 57346*, PEM R 2853*, 11.5 km S Steinkopf, 0.55 km E Hwy. N7 (2917Bd); JDV 1186, 12 km S Steinkopf, 5 km E (2917Bd); CM 119382, 4 km E Steinkopf (2917Bd); JDV 2575-77, 2601, 5576, TM 52760, 53388, ZMB 22894, 22897 [one of two specimens bearing this number], Steinkopf (2917Bc); CAS 186301-06, 67 km E Port Nolloth ( 2917 Bc ); TM 27701-04, 27707-08, Anenous Pass ( $29^{\circ} 13^{\prime} \mathrm{S}, 17^{\circ} 37^{\prime} \mathrm{E}$ ); TM $34094,30 \mathrm{mi}$ E Port Nolloth on road to Steinkopf (2917Ad); TM 18039-47, 20 miles E Port Nolloth (2917Ac); TM 35235-37, Farm Gemsbokvley ( $29^{\circ} 19^{\prime} \mathrm{S}, 17^{\circ} 08^{\prime}$ E); PEM R 12803, SAM 18556, Lekkersing (2917Aa); TM 27914,

Lekkersing ( $29^{\circ} 00^{\prime} \mathrm{S}, 17^{\circ} 06^{\prime} \mathrm{E}$ ); TM 53845, Kamma River above Springbokvlei ( $29^{\circ} 05^{\prime} \mathrm{S}, 17^{\circ} 05^{\prime} \mathrm{E}$ ); SAM 47705, Kammarivier ( $29^{\circ} 05^{\prime} 04^{\prime \prime} \mathrm{S}, 17^{\circ} 05^{\prime} 34^{\prime \prime} \mathrm{E}$ ); JDV N17880, 3 km W Springbok (2917Db); JDV 51180, N13980, N15080, 31 km E Springbok ( 2918 Ca ); TM 56211, Henkries ( $28^{\circ} 57^{\prime} \mathrm{S}, 18^{\circ} 06^{\prime} \mathrm{E}$ ); CAS 186366 , Lekkersing Rd., 30 km S jct. Eksteenfontein Rd. (2817Cc); TM 34206, 7 mi. SW Stinkfontein (2817Cc); TM 34273-74, 13 mi . E Stinkfontein towards Vioolsdrif (2817Cd); LSUMZ 57345, PEM R 11942, Uitpanspoortberg ( $28^{\circ} 57^{\prime} \mathrm{S}, 17^{\circ} 02^{\prime} 30^{\prime \prime}$ E); CAS 200056*, Lekkersing rd., 45.2 km S Alexander BaySendelingsdrif Rd. ( $28^{\circ} 47^{\prime} 04^{\prime \prime} \mathrm{S}, 17^{\circ} 00^{\prime} 24^{\prime \prime} \mathrm{E}$ ); TM 2806511.2 km S of Dolomite Peaks ( $28^{\circ} 47^{\prime} \mathrm{S}, 17^{\circ} 03^{\prime} \mathrm{E}$ ); TM 27871-72, Groenkloefrivier, 17.6 km SW Kubus ( $28^{\circ} 31^{\prime} \mathrm{S}$, $16^{\circ} 58^{\prime}$ E); PEM R12798, Kuboes (2816Bd); TM 34303, Hellskloof Pass, Richtersveld National Park (2816Bd); TM 22983, Sendelingsdrif, Richtersveld National Park ( $28^{\circ} 10^{\prime}$ S, $16^{\circ} 53^{\prime} \mathrm{E}$ ); TM 53850, Sendelingsdrif, Richtersveld National Park ( $28^{\circ} 05^{\prime} \mathrm{S}, 16^{\circ} 56^{\prime} \mathrm{E}$ ); SAM 43749-50, 4 unnumbered specimens, Little Namaqualand; JDV 1675, 2610, N15280, TM 13716-18, Namaqualand. Namibis: Lüderitz District: TM 27737, Skerpioenkop, Lüderitz District ( $27^{\circ} 46^{\prime} \mathrm{S}, 16^{\circ} 30^{\prime}$ E) [?]. Unidentified/Ambiguous localities: SAM 18798 ( 6 specimens), 18799 ( 2 specimens), 18800 ( 2 specimens), Bowesdorp; SAM 46930, Nauchas (presumably not Nauchas, Rehoboth District, Namibia). Unknown locality: JDV 1056-57, 1230, 2171, 2601, 15180, 32080, 77578, N53580. Additional records: South Africa: Northern Cape Province: Goegap Nature Reserve (Girard 1997); Approximately 10 km W Garies on road to Hondeklipbaai ( $30^{\circ} 35^{\prime} 36^{\prime \prime}$ S, $17^{\circ} 52^{\prime} 06^{\prime \prime}$ E) (pers. comm., M. Burger, September 2005; photo vouchers).

Diagnosis.- To 50.0 mm SVL (JDV 1473, 81478). Pachydactylus weberi may be distinguished from all other members of the P. serval/weberi group by the combination of the following characters: rostral (and rarely first supralabial) excluded from nostril; supranasals in variable contact; scales on dorsum of head smooth and flat, those on snout much larger than those of interorbital and parietal regions; dorsal scalation strongly heterogeneous, flattened, conical, or weakly keeled tubercles in 16-22 rows; thighs bearing at least some enlarged, often keeled tubercles; toes moderately short, toe pads somewhat expanded; typically 5 undivided lamellae beneath digit IV of pes; tail to $131 \%$ SVL, annulate, bearing whorls of flattened to keeled, pointed tubercles; adult pattern light brown to russet or pale orange with three light (white, pale yellow, buff, pinkish or ashy) bands (one on nape, two on trunk) with brown borders variably evident, at least nape band usually apparent, traces of body bands usually persist, even in very large specimens, but pattern as a whole often obscured by break-up of dark edges on cross bands and presence of dark markings in interstices between bands (Figs. 1, 13-18; see also Girard 2002); original tail boldly banded; juvenile pattern bold, one nape and two body bands, each pale with dark edges, bands usually with slightly wavy margins, some stray dark markings between bands (Figs. 3, 18-20; see also Visser 1984:51; Seufer 1991:124 top).

Distribution.- Distributed more or less continuously throughout areas of suitable rocky substrate in the western Northern Cape and northwestern Western Cape. Populations occur in the Cederberg, Bokkeveldberge and throughout Namaqualand (Figs. 21-22). At Kleinsee the species' range nearly reaches the coast. Inland the species occurs near the Hantamsberg and along the western slopes of the Roggeveldberge. It is also present at suitable sites in the Knersvlakte and has recently been collected in the Tankwa Karoo. In the north P. weberi occurs along the western side of the Richtersveld, in and on the flanks of the Vandersterrberge, reaching the Orange River at Sendelingsdrif. This species is nearly strictly limited to the Republic of South Africa, although a single specimen from Skerpioenkop, a southern outlier of the Aurusberg Mountains of southern Namibia is here tentatively referred to this taxon as well. Griffin (2000a) considered P. weberi as occurring around the Brandberg in northwestern Namibia. We examined no material referable to the $P$. weberi group from this area, but would predict that if a $P$. weberi group gecko other than $P$. fasciatus does occur there, it would represent an undescribed species.

Natural History.- Pachydactlyus weberi is almost strictly rupicolous and is found chiefly in association with narrow horizontal cracks, capstones, or exfoliating flakes (Visser 1984; Branch
1998). Rocky areas occupied include large outcrops or cliff faces (Fig. 23), but they are also common in small boulder clusters (Fig. 24) or even groups of rocks of less than $1 \mathrm{~m}^{3}$. They occur in sandstones, granites or other types of rocks, wherever erosion or fragmentation provides suitable shelter and thermal conditions. Visser (1984) reported that specimens were found on the ground under trash near Wallekraal.

Visser (1984) reported that the species generally lays eggs in January, but that near Bitterfontein, eggs ( $9.2 \times 6.7 \mathrm{~mm}$ ) are laid in August and that a very late group of eggs were found in May near Kharkams. Communal egg-laying sites have been reported (Visser 1984; Branch 1998). We have found many eggs in rock crevices or under capstones, but in captivity they are laid in sand (Girard 2002).

Mites (Geckobia namaquensis and G. capensis hastata) have been recorded from P. weberi (Lawrence 1936, 1951).

Diet in the wild is reported to include spiders, moths, and homopteran larvae (FitzSimons 1943; Branch 1998). Captive maintenance and reproduction, including copulatory behavior, as well as vocalization, have been reported on by Girard (2002) and Rösler (2005).

Conservation Status.- Pachydactylus weberi is a common species in most places where it occurs. Protected populations include those in the Cederberg Wilderness Area, Tankwa Karoo National Park, Goegap Nature Reserve, and Richtersveld National Park. The species may also occur in the Akkerandam and Oorlogskloof Nature Reserves. Effective protection is also afforded to this species on land controlled by DeBeers near Kleinsee and in the Spergebied of southern Namibia (Skerpioenskop population).

Remarks. - In specimens from the extreme northern portion of the range (Richtersveld localities: Hellskloof Pass, Groenkloofrivier, 13 km S Eksteenfontein) the dark margins of light bands are especially prominent and the adult pattern appears as alternating light and dark bands along the length of the trunk. Specimens from Calvinia are uniformly more robust than those from more coastal areas of Namaqualand. The status of these inland populations should be investigated further.

Barbour and Loveridge (1946) identified MCZ R 31573-74 as paratypes of Pachydactylus capensis gariesensis, with the locality "Garies to Kamiesberg, Little Namaqualand, South Africa." However, Hewitt (1932) indicated that specimens from this locality were received from Peers after the types. Thus, the MCZ specimens appear not to be true types. However, MCZ R 48142, which was not listed by Barbour and Loveridge (1946) as a type, was collected by B. Peers in October 1929 at Garies and may be one of the types, although this has not been confirmed. Hewitt (1932) had explicitly mentioned that there were nine syntypes under the number SAM 17953. In March 2005 we found a total of 13 specimens in two lots of ten and three, respectively, bearing this number. As measurements were provided for only a single specimen in the type description, it is not now possible to confirm the other types.

## Pachydactylus serval Werner, 1910 (Figs. 2, 25-29)

1910 P[achydacti/lus]. serval Werner, Denkschr: Med.-Nat. Ges. Jena 16:313, fig. 10 (Lectotype: ZMB 23121 [designated by implication by Loveridge 1947, see Bauer and Günther 1991] (Fig. 2): "Chamis, GroßNamaland" (see Remarks), August 1905. Paralectotype: ZMB 23122: same collection data as holotype.) 1910 P[achydactylus] serval Boulenger, Ann. S. Afr: Mus. 463.
1911 Pachydactylus serval Hewitt, Ann. Transvaal Mus. 3:45.
1911 Pachydactylus serval Sternfeld, Fauna dtsch. Kolon. 4(2):16.
1911 P[achydactylus]. serval Sternfeld, Mitt. Zool. Mus. Berlin 5:398.
1913 [Pachydactylus] serval Hewitt, Ann. Natal Mus. 2:483.
1927 [Pachydactylus] serval Hewitt, Rec. Albany Mus. 3:398.

1929 Pachydactylus serval Lawrence, J. S.W. Afr. Sci. Soc. 2:25.<br>1936 Pachydactylus purcelli Parker, Novit. Zool. 40:130.<br>1936 Pachydactylus serval Lawrence, Parasitology 28:38.<br>1938 Pachydactylus montanus onscepensis [part] FitzSimons, Ann. Transvaal Mus. 19:173.<br>1943 Pachydactylus serval FitzSimons, Mem. Transvaal Mus. 1:74.<br>1943 Pachydactylus purcelli [part] FitzSimons, Mem. Transvaal Mus. 1:65.<br>1943 Pachydactylus montanus onscepensis [part] FitzSimons, Mem. Transvaal Mus. 1:84.<br>1947 Pachydactylus serval [part] Loveridge, Bull. Mus. Comp. Zool. 98:388.<br>1951 Pachydactylus montanus onscepensis Lawrence, Ann. Transvaal Mus. 21:453.<br>1955 Pachydactylus serval [part] Mertens, Abhandl. Senckenberg. naturf. Ges. 490:48.<br>1965 Pachydactylus serval [part] Wermuth, Das Tierreich 80:123.<br>1966 [Pachydactylus serval] serval [part] McLachlan and Spence, Ann. Cape Prov. Mus. 5:155.<br>1966 [Pachydactylus serval] onscepensis [part] McLachlan and Spence, Ann. Cape Prov. Mus. 5:155.<br>1971 Pachydactylus serval serval [part] Mertens, Abhandl. Senckenberg. naturf. Ges. 529:42.<br>1982 Pachydactylus serval serval [part] Welch, Herpetology of Africa: 36.<br>1984 Pachydactylus serval serval [part] Visser, Landbouweekbl. 27 April 1984:48, fig. p. 51, middle.<br>1988 Pachydactylus s. serval Branch, Field Guide:207.<br>1991 Pachydactylus serval Bauer and Günther, Mitt. Zool. Mus. Berlin 67:294.<br>1991 [Pachydactylus] serval Kluge, Smithson. Herpetol. Inform. Serv. 85:23.<br>1993 [Pachydactylus] serval Kluge, Gekkonoid Lizard Taxonomy:25.<br>1994 Pachydactylus serval serval Welch, Lizards of the World 1:95.<br>1994 Pachydactylus s. serval Branch, Field Guide, 2nd ed.:207.<br>1998 Pachydactylus s. serval Branch, Field Guide, 3rd ed.:260.<br>2000 [Pachydactylus] serval serval Rösler, Gekkota 2:99.<br>2001 [Pachydactylus] serval Kluge, Hamadryad 26:21.<br>2003 Pachydactylus serval serval Griffin, Namibian Reptiles:37.<br>2005 P[achydactylus]. serval [part] Bauer and Lamb, Afr. J. Herpetol. 54:116.

Material examined. - Namibia: Lüderitz District: JDV 1933, 22 km N Rosh Pinah (2716Dc); Keetmanshoop District: CAS 193656, 31.6 km S Dassiefontein River Crossing, S. of Keetmanshoop (2718Bc); TM 41907-08, Farm Florida (2718Bc); 17738, Seeheim (2617Dd); ZFMK 32925-28, Daweb-Süd (2618Bc); JDV 3677, just N Keetmanshoop (2618Ca); JDV N39960, 3 km N Keetmanshoop (2618Ca); SAM 46690, 46750-53, 10 km N Keetmanshoop (2618Ca); SAM 46688-89, 20 km N Keetmanshoop (2618Ac); TM 17780, 17782-86, 28255, 33290, 37350, 41821-22, 42972, MCZ R 46805 (formerly TM 17781), Brukkaros Mountain (2517Dd); NMNW R 10500, Brukkaros Mountain at $25^{\circ} 54^{\prime} 56^{\prime \prime} \mathrm{S}, 17^{\circ} 46^{\prime} 56^{\prime \prime} \mathrm{E}$; NMNW R 136, TM 32866-67, Tses (2518Cc); Karasburg District: JDV 35880, btwn Noordover and Ai-Ais turnoff (2817Da or 2817 Db ); TM 42339, Fish River National Park (2717); NMNW R 8857*-58*, Ai-Ais Nature Reserve, ca. $3 \mathrm{~km} N$ Orange River ( $28^{\circ} 12^{\prime} 26^{\prime \prime} \mathrm{S}, 17^{\circ} 16^{\prime} 43^{\prime \prime} \mathrm{E}$ ); TM 54439, Fish River Canyon viewpoint $\left(27^{\circ} 35^{\prime} \mathrm{S}, 17^{\circ} 37^{\prime} \mathrm{E}\right)$; Bethanie District: TM 53214-15, Dam Huns 106 (2717Ac) TM 17717, 17719-21, 20 mi. E Konkiep (2617Dc); JDV 30780, 20 km N Bethanien (2617Aa); TM 17718, 32 km E Goageb Stn. ( $26^{\circ} 47^{\prime} \mathrm{S}$, $17^{\circ} 32^{\prime}$ E); PEM R 147, 222, 226, 2 mi from Konkiep on Rd. to Seeheim (2617Cc); AMB (MCZ Field) 38272-80, Konkiep ( $26^{\circ} 41^{\prime} 59^{\prime \prime} \mathrm{S}, 17^{\circ} 13^{\prime} 16^{\prime \prime} \mathrm{E}$ ); TM 48375, Farm Kunjas (2516Dd); MCZ R 163287, 20 km SW Helmeringhausen ( 2616 Ba ); TM 28423-26, Farm Tiras, 49.6 km S of Helmeringhausen $\left(26^{\circ} 10^{\prime} \mathrm{S}\right.$, $16^{\circ} 36^{\prime}$ E); PEM R 278, 280-87, 289, 5 mi . N Chamis (2516Dd); ZMB 23121 (lectotype of P. serval), 23122 (paralectotype of P. serval), Chamis (2516Dd); TM 17678-79, 17681, MCZ R 46806 (formerly TM 17680), Barby (2516Dc); JDV 36080, Helmeringhausen (2516Dd); Maltahöhe District: PEM R 136, 139-40, Naudas (2516Bc); PEM R 129-30, 137, Osis (2516Bd); TM 48382, Farm Duisib (2516Bc); TM 17580, Maltahöhe ( $24^{\circ} 50^{\prime} \mathrm{S}, 16^{\circ} 59^{\prime} \mathrm{E}$ ); Swakopmund District: TM 55490, within 40 km from Swakopmund-Usakos (2214Da) [probably in error]; Mariental District: TM 41791, 41823, Farm Hardap (2417Bd); PEM R 6035, 8862, Hardap Dam ( $24^{\circ} 23^{\prime} \mathrm{S}, 17^{\circ} 54^{\prime} \mathrm{E}$ ); TM 53952, Hardap Dam ( $24^{\circ} 30^{\prime} \mathrm{S}, 17^{\circ} 50^{\prime} \mathrm{E}$ ); TM 56656, Farm Keikanchab $91\left(24^{\circ} 37^{\prime} \mathrm{S}, 17^{\circ} 52^{\prime} \mathrm{E}\right)$; SMF 45699, Gaitsabis (2417Da); TM 56657, Mariental ( $\left.24^{\circ} 38^{\prime} \mathrm{S}, 17^{\circ} 58^{\prime} \mathrm{E}\right)$. Unknown LOCALITY: JDV 31080, JDV 36180.

Figure 1. Lectotype of Pachydactylus weberi (ZMA 11046) from Klipfontein, Little Namaqualand (Northern Cape Province), South Africa as figured by Roux (1907) in the type description.

Figure 2. Lectotype of Pachydactylus serval (ZMB 23121) from Farm Chamis, Great Namaqualand (Bethanie District), Namibia as figured by Werner (1910) in the type description.

Figure 3. Juvenile Pachydactylus weberi (now MCZ R 21019) from Kammagas, Northern Cape Province, South Africa originally figured by Werner (1910) as P. fasciatus.

Figure 4. Specimens referred to Pachydactylus purcelli by Methuen and Hewitt (1914: text figure 15): adult (TM 3102, between Kraikluft and Alt Wasserfall, Keetmanshoop District, Namibia). juvenile (TM 3090, Farm Pieterskloof, Kraikluft, Keetmanshoop District, Namibia), and embryo (TM 3095, Farm Pieterskloof, Kraikluft, Keetmanshoop District, Namibia), ostensibly illustrating the ontogenetic change in color pattern in this species. In reality, only the adult specimen is referable to this species. The younger specimens are $P$. montanus.

Figure 5. Series of adult and subadult specimens of Pachydactylus fasciatus specimens illustrating variation in the boldness of the broad, saddle-shaped bands in this species. From left to right: CAS 214675 ( 48.0 km west of Kamanjab, Khorixas District. Namibia). CAS 176094 (100.6 km west of Kamanjab, Khorixas District, Namibia), CAS 206936 ( 10 km east of Spitzkop turnoff, Karibib District, Namibia), CAS 214677 ( 48.0 km west of Kamanjab. Khorixas District, Namibia). Scale bar $=20$ mm . Photo by A.M. Bauer.

Figure 6. Adult Pachydactilus fasciatus (CAS 214675) from 48.0 km west of Kamanjab. Khorixas District. Namibia in life. Photo by T. Lamb.

Figure 7. Subadult Pachydactylus fasciatus (CAS 214677) from 48.0 km west of Kamanjab. Khorixas District. Namibia in life. Photo by T. Lamb.

Figure 8. Hatchling Pachydacrilus fasciatus (CAS 193681) from 59.3 km west of Kamanjab. Khorixas District, Namibia in life. Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 9. Juvenile Pachydactylus fasciatus (TM 79074) from Warmbad, Karasburg District, Namibia. This specimen represents the only confirmed record of this species from extreme southern Namibia. Photo courtesy of W.D. Haacke.


Figure 10. Map of western southern Africa with selected reference points and regions mentioned in the text indicated. Black text: physical features, mountains (small font), mountain ranges, physiographic regions (small font, italics), large physiographic regions (large font, italics), countries (large font, all capitals). Blue lines and text: rivers (lower courses only shown). Red text: towns and other named places. MODIS imagery from the Global Land Cover Facility (http://www.landcover.org).

Figure 11. Distribution map for endemic Namibian and Botswanan species of the Pachydactylus weberi group and P. sansteynae: P. fasciatus (red), P. acuminatus (black), P. kobosensis (pink), P. werneri (dark blue), P. reconditus, sp. nov. (yellow), P. waterbergensis (light blue), P. otaviensis, sp. nov. (olive), P. tsodiloensis (bright green), P. sansteynae (white). Question marks indicate questionable but plausible localities (see respective species accounts for further comments). Base map from NOAA National Geophysical Data Center.

Figure 12. Typical habitat of Pachydactylus fasciatus in mopane (Colophospermum mopane) dominated savanna west of Kamanjab, Namibia. The species is terrestrial and often occupies daytime retreats under calcrete boulders (foreground). Photo by A.M. Bauer.

Figure 13. Syntypes of Pachydactylus capensis gariesensis (SAM 17953 part) from Garies, Northern Cape Province, South Africa as figured by Hewitt (1932: plate VI). Position of figures relative to each other has been modified in this reproduction.

Figure 14. Representative adult specimens of Pachydactylus weberi illustrating variation in dorsal color pattern. From left to right: CAS 193327 (11.5 km S Steinkopf, Northern Cape Province, South Africa). CAS 186366 (Lekkersing road, 30 km S junction Eksteenfontein road, Northern Cape Province, South Africa), CAS 206823 (Brandberg, Farms Kourootje and Kap Vley, Northern Cape Province, South Africa). Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 15. Adult Pachydactylus weberi from Kleinsee. Northern Cape Province, South Africa illustrating retention of the bold tail banding and some obfuscation of the juvenile three-banded pattern. Photo courtesy of R.D. Babb.


Figure 16. Adult Pachydactylus weberi from approximately 10 km west of Garies, on road to Hondeklipbaai, Northern Cape Province, South Africa ( $30^{\circ} 35^{\prime} 36^{\prime \prime}$ S, $17^{\circ} 52^{\prime} 06^{\prime \prime} \mathrm{E}$ ) illustrating relatively faded dorsal pattern. Photo courtesy of M. Burger.

Figure 17. Adult Pachydactylus weberi from Boskloof, near Citrusdal, Western Cape Province, South Africa illustrating a multi-banded pattern seen only in some members of the southernmost populations of this species. Photo courtesy of J.D. Visser.

Figure 18. Adult and juvenile speciens of Pachydactylus weberi from Kleinsee, Northern Cape Province, South Africa ( $29^{\circ} 40^{\prime} 04^{\prime \prime} \mathrm{S}, 17^{\circ} 04^{\prime} 36^{\prime \prime} \mathrm{E}$ ) illustrating clear retention of the juvenile three-banded pattern in the adult and relatively bright coloration. Photo courtesy of M. Burger.

Figure 19. Hatchling Pachydactylus weberi (TM 34273) from 13 mi ( 21 km ) E Stinkfontein (Eksteenfontein), Northern Cape Province, South Africa illustrating the typical banded pattern of hatchlings and juveniles of this species. Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 20. Hatchling Pachydactylus weberi with eggs of multiple clutches, from near Nigramoep, Northern Cape Province, South Africa. Photo courtesy of J.D. Visser.

Figure 21. Map of western South Africa with selected reference points and regions mentioned in the text indicated. Black text: physical features, mountain ranges, physiographic regions (small font, italics), provinces (large font, all capitals). Blue text: rivers. Red text: towns and other named places. Base map from NOAA National Geophysical Data Center.

Figure 22. Distribution map for South African and southern Namibian species of the Pachydactylus weberi group: $P$. weberi (dark blue), $P$. robertsi (light blue), $P$. monicae. sp. nov. (red), $P$. visseri, sp. nov. (white), P. mclachlani, sp. nov. (yellow), $P$. goodi, sp. nov. (brown). Base map from NOAA National Geophysical Data Center.


Figure 23. Habitat of Pachydactilus weberi near Van Rhynsdorp, Western Cape Province, South Africa. Here, and in the Cedarberg to the south, this species typically occupies crevices between blocks of sandstone or other narrow fissures. Photo courtesy of R.A. Sadlier.

Figure 24. Typical habitat of Pachydactylus weberi in low, exfoliating granite boulders in sandy plains south of the Richtersveld, on road to Lekkersing, Northern Cape Province, South Africa. Here the species typically uses downward opening exfoliations and capstones as retreat sites. Photo by A.M. Bauer.

Figlre 25. Representative adult specimens of Pachydactylus serval illustrating variation in dorsal color pattern. From left to right: TM 48382 (Farm Duisib, Maltahöhe District. Namibia). TM 28423 (Farm Tiras. Bethanie District. Namibia), TM 41821 (Brukkaros Mountain, Keetmanshoop District, Namibia). Scale bar $=20$ mm . Photo by A.M. Bauer.

Figure 26. Adult Pachidactylus serval from southwestern Namibia. Photo courtesy of R.D. Babb.

Figlre 27. Subadult Pachydactilus serval from Hardap Dam. Mariental District, Namibia illustrating transitional pattern from juvenile banding to adult spotting. Photo by W.R. Branch.

Figure 28. Juvenile specimens of Pachydactylus serval from Brukkaros Mountain. Keetmanshoop District. Namibia (left: TM 17786. right: TM 28255) illustrating the pale nape band and sacral/hindlimb marking typical of hatchlings and juveniles of this species. Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.

Figlre 29. Hatchling Pachydactylus serval from Bethanie, Bethanie District, Namibia, illustrating contrasting black and ashy color pattern and dark tail and distal hindlimbs. Photo courtesy of J.D.Visser.

Figlre 30. Map of Southern Namibia and adjacent regions with selected reference points and regions mentioned in the text indicated. Black text: physical features (small font), mountain ranges (small font. italics), large physiographic regions (large font. italics), countries (large font. all capitals). Blue text: rivers. Red text: towns and other named places. MODIS imagery from the Global Land Cover Facility (http://www.landcover.org).


Figure 31. Distribution map for species of the Pachydactylus serval group: $P$. serval (red), P. purcelli (dark. blue), P. montanus (yellow), P. griffini, sp. nov. (pink), $P$. carinatus, sp. nov. (black). Question mark indicates questionable but plausible locality (see P. purcelli species account for further comments). Base map from NOAA National Geophysical Center.

Figure 32. Habitat of Pachydactylus serval near the type locality of the species, 10.1 km southeast of Helmeringhausen, Bethanie District, Namibia, with the Konkiep River valley beyond the end of the road and the Schwarz Rand in the distance at left and center. Photo by A.M. Bauer.

Figure 33. Syntypes (SAM 1260-61) of Pachydactylus purcelli from "Touw's River" (Touwsrivier), Western Cape Province, South Africa. Both specimens are extremely soft and in poor condition. Photo by A.M. Bauer.

Figure 34. Holotype (ZMB 23453) of Pachydactylus pardus from Warmbad, Karasburg District, Namibia. Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 35. Representative adult South African specimens of Pachydactylus purcelli illustrating variation in dorsal color pattern. From left to right: CAS 198295 (Oukloof Pass, Western Cape Province, South Africa), CAS 199995 ( 15 km northwest of Fraserburg. Northern Cape Province, South Africa), CAS 198294 (Oukloof Pass, Western Cape Province. South Africa). CAS 180388 ( 2 km west of entrance to Anysberg Reserve, Western Cape Province. South Africa). The small specimen on the far right retains clear evidence of the juvenile banding pattern. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 36. Pachydactrlus purcelli (CAS 231887) from Farm Narudas, Karasburg District. Namibia. Although this is the largest specimen of this species examined ( 50.8 mm SVL), elements of the juvenile banded pattern remain. This trait is highly variable but more common in northern populations than in those from the Karoo and Little Karoo. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figlre 37. Adult Pachydactylus purcelli from Kokerboomwoud, 8 km south of Kenhardt. Northern Cape Province. South Africa ( $29^{\circ} 24^{\prime} 22^{\prime \prime} \mathrm{S}, 21^{\circ} 06^{\prime} 18^{\prime \prime} \mathrm{E}$ ) exhibiting retention of the typical three-banded juvenile pattern. Photo courtesy of M. Burger.


Figure 38. Pachydactylus purcelli (CAS 231887) from Farm Narudas, Karasburg District, Namibia. As is typical for this species, the body is virtually atuberculate except for a few tiny tubercles in the sacral region. Photo by A.M. Bauer.

Figure 39. Subadult specimens of Pachydactylus purcelli. From left to right: CAS 126035 (19 miles southwest of Upington on road to Kiemoes, Northern Cape Province, South Africa), TM 82319 ( 10 km from Duine Municipal Site, Northern Cape Province, South Africa), TM 15921 (Kakamas, Northern Cape Province, South Africa). Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 40. Juvenile Pachydactylus purcelli from 28.3 km east of Pofadder, Northern Cape Province, South Africa (left: CAS 203490, right: CAS 203493). Hatchlings and juveniles bear three transverse bands and usually show little evidence of spotting. Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 41. Especially vibrantly colored juvenile of Pachydactylus purcelli from Farm Karos, Northern Cape Province, South Africa (2821Bc). Photo courtesy of W.D. Haacke.

Figure 42. Habitat of Pachydactylus purcelli at Molteno Pass, Nuweveldberge, Western Cape Province, South Africa. Specimens were found in retreats within larger cliff faces as well as in crevices in the smaller boulder piles in the foreground. Photo by W.R. Branch.

Figure 43. Habitat of Pachydactylus purcelli at Farm Narudas, Karasburg District, Namibia. At this locality it was found under slabs of rock on rock in and adjacent to the dry river bed figured. Photo by A.M. Bauer.

Figure 44. Holotype of Pachydactilus montanus (TM 3080) from Lord Hill's Peak, Keetmanshoop District, Namibia, as illustrated by Hewitt (1927).


Figure 45. Holotype (left, PEM 16050) and non-type specimen mentioned in type description (right, PEM. 16051) of Pachydactylus montanus onscepensis from "Onscephans" (Onseepkans), Northern Cape Province. South Africa. Scale bar $=20$ mm. Photo by A.M. Bauer.

Figure 46. Representative adult specimens of Pachydactylus montanus illustrating variation in dorsal color pattern. From left to right: CAS 176254 ( 7 km north of Grabwasser, Karasburg District, Namibia), CAS 201859 ( 5.0 km south of Onseepkans, Northern Cape Province. South Africa). TM 15920, TM 15916 (both Kakamas, Northern Cape Province, South Africa), TM 68557 (Riemvasmaak, Northern Cape Province, South Africa), CAS 201864 (Farm Kinderzitt, Karasburg District. Namibia), CAS 176253 ( 7 km north of Grabwasser, Karasburg District, Namibia). Note varying degree of tuberculation between specimens. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 47. Live specimen of adult Pachydactylus montanus from 79.5 km south of Keetmanshoop, Karasburg District, Namibia. Photo courtesy of P. Freed.

Figure 48. Live specimen of adult Pachydactylus montanus from between Grünau and Klein Karas, Karasburg District, Namibia. Photo courtesy of J.D. Visser.

Figure 49. Live specimen of adult Pachydactylus montanus from just south of Onseepkans, Northern Cape Province, South Africa. Photo by T. Lamb.

Figure 50. Juvenile specimens of Pachydactylus montanus illustrating the species-specific character of four pale. dark-edged transverse bands between nape and sacrum. From left to right: TM 36809 (Farm Eendoorn, Karasburg District, Namibia), TM 36758 (Farm Schuitdrif, Northern Cape Province, South Africa). CAS 201861 ( 3.5 km north of Tantalite Valley, Karasburg District, Namibia). Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.


Figure 51. Juvenile Pachydactylus montanus from Savanna Guest Farm, Keetmanshoop District, Namibia ( $2718 B c$ ), exhibiting the series of four pale transverse bands typical of juveniles of this species. Photo courtesy of T. Gamble.

Figure 52. Habitat of Pachydactylus montanus in Great Karasberg Mountains, Keetmanshoop District, Namibia (2718Bc). At this locality P. montanus was found in crevices in the larger rock slabs and boulders along the base of the cliff. Photo by A.M. Bauer.

Figure 53. Habitat of Pachydactylus montanus on Savanna Guest Farm, Keetmanshoop District, Namibia (2718Bc). At this locality P. montanus was found under exfoliatiations and beneath large, thin, flat slabs in boulder piles and around isolated rocky hills. Photo courtesy of T. Gamble.

Figure 54. Lectotype (PEM 16049) and paralectotype (PEM 16048) of Pachydactylus capensis wemeri from "Khan River," Swakopmund District, Namibia. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 55. Representative adult and subadult specimens of Pachydactylus werneri illustrating variation in dorsal color pattern. From left to right: TM 42901 (Gobabeb, Swakopmund District, Namibia), TM 31758, TM 31757 (both Palmenhorst on Swakop River, Swakopmund District, Namibia), TM 57276 (Farm Arbeid Adelt, Maltahöhe District. Namibia). Note the relatively long limbs, long head, and small, white tubercles. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 56. Adult specimen of Pachydactylus wemeri (MCZ R 183707) from north bank of Swakop River at $22^{\circ} 38^{\prime} 14^{\prime \prime} \mathrm{S}, 14^{\circ} 43^{\prime} 39^{\prime \prime} \mathrm{E}$. Note the long digits typical of this species. Photo by A.M. Bauer.

Figure 57. Juvenile Pachydactylus wemeri from Homeb, Swakopmund District, Namibia. Note the raised scales around the nostrils. Photo courtesy of J. Boone.

Figure 58. Representative adult specimens of Pachydactjlus kobosensis illustrating variation in dorsal color pattern. Top: CAS 223903 ( 5.0 km south of Kobos, Rehoboth District, Namibia), bottom: JDV 39880N (Rehoboth. Rehoboth District, Namibia). Note the very fine dorsal scalation and minute tubercles. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.


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Figure 59. Adult specimen of Pachydactylus kobosensis (CAS 223903) from 5.0 km south of Kobos, Rehoboth District, Namibia. This specimen and several others were found in crevices in isolated rock koppies in open savanna. Photo courtesy of R.A. Sadlier.

Figure 60. Adult specimen of Pachydactylus kobosensis from Nauchas, Windhoek District, Namibia. Photo courtesy of J.D. Visser.

Figure 61. Hatchling Pachydactylus kobosensis (left: JDV 54780, right: JDV 54680) from the vicinity of Kobos. Rehoboth District, Namibia exhibiting the very bold banded pattern. Juveniles begin to change to the adult pattern relatively early in life. Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 62. Holotype of Pachydactylus robertsi (TM 17854) from Farm Kraikluft, Keetmanshoop District, Namibia. SVL of specimen 42 mm . Photo by A.M. Bauer.

Figure 63. Pachydactylus robertsi (NMNW 6697) from Farm Kuchanas, Keetmanshoop District. Namibia. The large. partly imbricating dorsal tubercles are diagnostic of this species. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 64. Life photograph of Pachydactylus robertsi (NMNW 6697) from Farm Kuchanas. Keetmanshoop District, Namibia. The yellowish rims of the orbit and bright white of the supralabials are clearly visible. Photo courtesy of M. Griffin.

Figure 65. Life photograph of Pachydactilus robertsi (CM 119308) from 79.5 km south of Keetmanshoop. Keetmanshoop District, Namibia. Photo courtesy of P. Freed.


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Figure 66. Adult syntype (TM 17722) of Pachydactylus weberi acuminatus from Goageb Station, Bethanie District, Namibia. SVL of specimen 42 mm . The blank area near the tail base is masking an area of glare. Photo by A.M. Bauer.

Figure 67. Subadult syntypes (TM 17689-91, 17693-95) of Pachydactylus weberi acuminatus from 8 miles west of Aus. Approximate SVLs of specimens 30-37 mm . Photo by A.M. Bauer.

Figure 68. Adult and subadult specimens of Pachydactylus acuminatus. From left to right: JDV 30580 ( 5 km north of Aus, Luideritz District, Namibia), JDV 1930, 1932 (both 158 km east of Lüderitz, Lüderitz District, Namibia). The three juvenile pale bands are still evident in all specimens, but the intervening spaces become spotted, complicating the dorsal pattern. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 69. Hatchling Pachydactylus acuminatus. From left to right: JDV 26380 ( 20 km southwest of Helmeringhausen, Bethanie District, Namibia), JDV 30980 (Farm Houmoed. Bethanie District, Namibia), JDV 26680 ( 20 km south of Helmeringhausen. Bethanie District, Namibia). The left and center specimens illustrate the typical three-banded pattern of hatchlings and young juveniles. That on the right has four bands. Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 70. Juvenile Pachydactylus acuminatus (JDV 35280 ) from 20 km southwest of Helmeringhausen, Bethanie District, Namibia. Note the decrease in tubercle size on the anterior third of the body. The Photo courtesy of J.D. Visser.

Figure 71. Subadult Pachydactylus tsodiloensis (captive. from stock from Tsoldilo Hills, Botswana) showing the large tubercles and typical five-banded pattern of this species. Photo courtesy of M. Barts.

Figure 72. Life photograph of the holotype of Pachydactylus waterbergensis (NMNW R 6698) from Onjoka Settlement. Waterberg Plateau Park, Otjiwarongo District. Namibia, illustrating a five-banded pattern on the dorsum between nape and sacrum. Photo courtesy of M. Griffin.


Figure 73. Paratype of Pachydactylus waterbergensis (TM 38268) from the Waterberg, Otjiwarongo District, Namibia. Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 74. Specimen of Pachydactylus waterbergensis from the Waterberg Plateau, Otjiwarongo District, Namibia illustrating a six-banded condition. Photo courtesy of M. Barts.

Figure 75. Holotype of Pachydacţlus reconditus, sp. nov. (TM 32838), adult female, from Windhoek. Windhoek Distirct, Namibia, showing large, but non imbricating dorsal tubercles. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 76. Paratypes of Pachydactylus reconditus, sp. nov. From left to right: CAS 231886 (Oanab Dam, Rehoboth Distirct. Namibia), TM 41993. 41994 (both Farm Komuanab, Karibib Distirct, Namibia). The two adult specimens illustrate a lessstrongly spotted individual with relatively discrete nape band (left), and a more strong-ly-spotted individual with a less discrete nape band (center). The juvenile at right has three very pale trunk bands, which do not appear to be present in hatchlings. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 77. Life photo of Pachydactylus reconditus, sp. nov. (CAS 231886) from Oanab Dam. Rehoboth Distirct. Namibia. Photo by W.R. Branch.

Figure 78. Life photo of Pachydactylus reconditus, sp. nov. from Windhoek, Windhoek Distirct, Namibia. Note the striking similarity to P. robertsi (Figure 65). Photo courtesy of M. Barts.


Figure 79. Hatchling Pachydactylus reconditus, sp. nov. (NMNW R number pending) from Klein Windhoek. Windhoek Distirct, Namibia showing the typical pale nape band and patternless dorsum of the young of this species. Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 80. Juvenile specimen of Pachydactylus reconditus, sp. nov. (JDV 3013) from junction Otjimbingwe road and Swakopmund-Windhoek road. Karibib District, Namibia. Photo courtesy of J.D. Visser.

Figure 81. Juvenile specimen of Pachydactylus reconditus, sp. nov. (CM 115642) from Windhoek, Windhoek Distirct, Namibia. Photo courtesy of P. Freed.

Figure 82. Holotype of Pachydactilus monicae, sp. nov. (CAS 200034), adult male, from Sendelingsdrif, Richtersveld National Park. Northern Cape Province, South Africa. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 83. Life photo of holotype of Pachydactylus monicae, sp. nov. (CAS 200034) from Sendelingsdrif, Richtersveld National Park. Northern Cape Province, South Africa. The pale dorsal coloration is typical of most specimens of this species. Photo by W.R. Branch.

Figure 84. Adult paratype of Pachydactylus monicae, sp. nov. (left: TM 33806) from Swartpoort. Richtersveld National Park, Northern Cape Province, South Africa, and subadult specimen (right: TM 41854) from Farm Holoog. Karasburg District, Namibia. These specimens represent the extremes of fading and boldness, respectively, of the adult banding pattern of P. monicae. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figlre 85. Juvenile specimens of Pachydactilus monicae. sp. nov. Left: CAS 200079 (paratype). Sendelingsdrif. Richtersveld National Park, Northern Cape Province. South Africa) and right: TM 41854. Farm Holoog. Karasburg District, Namibia. Juveniles from the Richtersveld accumulate dark markings in the spaces between the pale dorsal transverse bands whereas those from Farm Holoog retain nearly immaculate interspaces throughout life. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.


Figure 86. Juvenile (left: CAS 193419, above Springbokvlakte, Richtersveld National Park, Northern Cape Province, South Africa) and hatchling (right: TM 32830 , Ai-Ais, Karasburg District, Namibia) specimens of Pachydactylus monicae, sp. nov. The dark dorsal background color is typical only of hatchlings and younger juveniles. Older juveniles always exhibit the very bold, dark-edged banding seen on the specimen to the left. Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 87. Freshly euthanized juvenile of Pachydactylus monicae, sp. nov. from the Fish River Canyon, Karasburg District, Namibia. The yellowish color of the pale transverse bands and grayish background color of the dorsum both fade in older specimens. Photo courtesy of W.D. Haacke.

Figure 88. Habitat of Pachydactylus monicae, sp. nov. along the south bank of the Orange River near Sendelingsdrif. Richtersveld National Park, Northern Cape Province, South Africa. In the Richtersveld this species is chiefly terrestrial and is found under natural and anthropogenic debris along the riverine corridor. Photo by A.M. Bauer.

Figure 89. Habitat of Pachydactylus monicae, sp. nov. in the Fish River Canyon, Lüdertiz and Karasburg Districts, Namibia. This species occurs chiefly in mesic habitats under debris or in boulder crevices near the valley bottom. Photo by A.M. Bauer.

Figure 90. Holotype of Pachydactylus griffini, sp. nov. (CAS 125855), subadult female, from 4 miles northwest of Aroab on road to Keetmanshoop. Keetmanshoop District, Namibia. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 91. Adult paratypes of Pachydactylus griffini. sp. nov. illustrating the range of variation in dorsal color pattern. From left to right: CAS 186294, adult male (Farm Narudas, Karasburg District. Namibia), CAS 125854, adult female (4 miles northwest of Aroab on road to Keetmanshoop. Keetmanshoop District, Namibia), MCZ R 163286. adult male (between Narubis and Aroab, Keetmanshoop District, Namibia). Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 92. Juvenile paratypes of Pachdactilus griffini, Left: CAS 186295 (Farm Narudas, Karasburg District. Namibia), right: TM 3099 (Narudas Süd. Karasburg District. Namibia). The spotted pattern of juveniles of this species is unique among members of the Pachydacnlus serval/weberi clade. Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 93. Holotype of Pachydactylus mclachlani, sp. nov. (NMNW R 10499). adult male, from Noordoewer. Karasburg District. Namibia. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figlre 94. Adult female paratype of Pachydacrylus molachlani, sp. nov. (CAS 186293). from Farm Narudas. Karasburg District. Namibia. This specimen exhibits a particularly complex pattern in which the transverse banding pattern is obscure. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

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Figure 95. Adult female paratypes of Pachydactylus mclachlani, sp. nov. Left: TM 54735 (Farm Sperlingsputs, Karasburg District, Namibia), right: CM 119309 ( 79.5 km south of Keetmanshoop, Keetmanshoop District, Namibia). Both specimens retain the pale nape band and some trace of the transverse body bands seen in juveniles. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 96. Life photo of adult female paratype of Pachydactylus mclachlani, sp. nov. (TM 54735) from Farm Sperlingsputs, Karasburg District, Namibia. The caudal tubercles are particularly pronounced in this and other specimens from near the Orange River. Photo courtesy of W.H. Haacke.

Figure 97. Life photo of paratypes of Pachydactylus mclachlani, sp. nov.: CM 119309 (adult female) and CM 119311 (juvenile) both from 79.5 km south of Keetmanshoop, Keetmanshoop District, Namibia. The color pattern of the juvenile is strikingly similar to that of $P$. carinatus, sp. nov. The nape and postaxillary bands and the pale scaral patch of the juvenile can still be discerned in the adult, despite the fragmentation of the dark interspaces. Photo courtesy of P. Freed.

Figure 98. Juvenile paratypes of Pachydactylus mclachlani, sp. nov. From left to right: CAS 186287 (Farm Narudas. Karasburg District, Namibia), CM 119310, 119311 (both 79.5 km south of Keetmanshoop. Keetmanshoop District, Namibia). All exhibit the narrow postaxillary band, wider nape band, and pale sacral region typical of hatchlings and juveniles of this species. Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 99. Kokerboon-dominated habitat of Pachydactylus mclachlani, sp. nov. in the Orange River valley. This species occurs in association with a variety of rock types, often in small boulder piles or outcrops. Photo by A.M. Bauer.

Figure 100. Xeric habitat of Pachydactylus melachlani, sp. nov. along the Orange River valley, Karasburg District. Namibia (Northern Cape Province, South Africa across river). Photo by A.M. Bauer.

Figure 101. Holotype of Pachydactrlus carinatus, sp. nov. (CAS 201908), adult female, from 13.3 km east of Oenna Mine. Richtersveld National Park, Northern Cape Province, South Africa. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 102. Representative adult specimens of Pachydactylus carinatus, sp. nov. illustrating variation in dorsal color pattern. From left to right: CAS 201910 (adult male, Richtersveld National Park at $28^{\circ} 02^{\prime} 41^{\prime \prime}$ S. $17^{\circ} 05^{\prime} 40^{\prime \prime} \mathrm{E}$, Northern Cape Province. South Africa). CAS 201913 (adult male. 8.1 km south of Oenna Mine, Richtersveld National Park. Northern Cape Province, South Africa). TM 27949 (subadult male, 15 km northeast of Stinkfontein [Eksteenfontein], Northern Cape Province. South Africa). Scale bar $=20 \mathrm{~mm}$. Photo A.M. Bauer.


Figure 103. Life photo of Pachydactylus carinatus, sp. nov. from Goodhouse, Northern Cape Province. The small, but prominent yellow tubercles typical of this species are clearly evident. Photo by T. Lamb.

Figure 104. Juvenile specimens of Pachydactylus carinatus, sp. nov. showing prominent nape band. Left: TM 25139 (Numees Mine, Richtersveld National Park, Northern Cape Province, South Africa, right: CAS 193392 ( 22.8 km east of Sendelingsdrif, Richtersveld National Park, Northern Cape Province, South Africa). Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 105. Juvenile specimen of Pachydactylus carinatus, sp. nov. from the Richtersveld National Park, Northern Cape Province, South Africa showing the species-specific bright orange tail. Juveniles of this species are similar in color pattern to both P. serval (Figure 29) and P. mclachlani (Figure 97). Photo by W.R. Branch.

Figure 106. Habitat of Pachydactylus carinatus, sp. nov. near Halfmens Pass, Richtersveld National Park, Northern Cape Province, South Africa. Here the species occurs in narrow crevices and under capstones. Photo by A.M. Bauer.

Figlre 107. Habitat of Pachydactrlus carinatus, sp. nov. on road to Oenna Mine in the central Richtersveld National Park, Northern Cape Province, South Africa. It occupies all types of crevices as long as they are narrow and are protected from moisture. Photo by A.M. Bauer.

Figure 108. Holotype of Pachydactilus visseri, sp. nov. (CAS 201874), adult male. from Ai-Ais Nature Reserve. Karasburg District. Namibia. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 109. Paratypes of Pachydacţlus visseri. sp. nov. Left: TM 50110, adult male (Ai-Ais, Karasburg District. Namibia), right: TM 35455, adult female ( 10 miles northwest of Fish River mouth. Karasburg District, Namibia). These specimens represent the seven- and six-banded patterns of this species, respectively. Scale bar $=20$ mm . Photo by A.M. Bauer.

Figure 110. Life photo of Pachydactylus visseri. sp. nov. from the Fish River Canyon. Karasburg District. Namibia. Photo courtesy of W.D. Haacke.

Figure 111. Juvenile specimen of Pachydact/lus visseri, sp. nov. (CAS 201877) from Ai-Ais Nature Reserve. Karasburg District. Namibia. Juvenile and adult dorsal patterns are identical in this species. Scale bar $=10 \mathrm{~mm}$. Photo by A.M. Bauer.


Figure 112. Habitat of Pachydactylus visseri, sp. nov. along the lower Orange River. View from Skilpadberg, Lüderitz District, Namibia towards Brandkaross, Northern Cape Province, South Africa. Most specimens have been found under exfoliating flakes of granite or in narrow rock crevices. Photo by A.M. Bauer.

Figure 113. Holotype of Pachydactylus goodi, sp. nov. (TM 27962), adult male, from 10 km south of Vioolsdrif, Northern Cape Province, South Africa. Scale bar = 20 mm . Photo by A.M. Bauer.

Figure 114. Adult paratypes of Pachydactylus goodi, sp. nov. Left: TM 84505, female (Farm Aggenys, Northern Cape Province. South Africa), right: CAS 231878, male ( 77 km east of Springbok, Northern Cape Province, South Africa). Scale bar $=$ 20 mm . Photo by A.M. Bauer.

Figure 115. Adult male paratype of Pachydactylus goodi, sp. nov. (CAS 231878) from 77 km east of Springbok, Northern Cape Province, South Africa. Note the white patches on the proximal portions of the forelimbs. Photo courtesy of J.D. Visser.

Figure 116. Juvenile paratype of Pachydactylus goodi, sp. nov. (TM 29707) from 10 km south of Vioolsdrif, Northern Cape Province, South Africa. Scale bar = 10 mm . Photo by A.M. Bauer.

Figure 117. Holotype of Pachydactylus otaviensis, sp. nov. (TM 45097), adult male, from Farm Uithoek. Tsumeb District. Namibia. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 118. Paratypes of Pachydactylus otaviensis, sp. nov. Left: TM 85002, juvenile, right: TM 85000, adult male (both Farm Varianto, Tsumeb District, Namibia). Note the large, pointed cloacal spurs on the adult paratype. Scale bar $=20$ mm . Photo by A.M. Bauer.


Figure 119. Representative adult specimens of Pachydactylus sansteynae illustrating differences in degree of dorsal pigmentation. Left: CAS 214767 (north bank of Huab River at Huab River Bridge, Skeleton Coast National Park, Khorixas District, Namibia), right: CAS 214589 ( 1 km south of Huab River Bridge, Skeleton Coast National Park, Khorixas District, Namibia). Note the superficial similarity in dorsal pattern to some members of the $P$. serval group. Scale bar $=20 \mathrm{~mm}$. Photo by A.M. Bauer.

Figure 120. Pachydactylus sansteynae (CAS 214589) from 1 km south of Huab River Bridge. Skeleton Coast National Park. Khorixas District, Namibia. Note the large, pointed cloacal spurs and the small, keeled tubercles. Photo courtesy of R.D. Babb.

Figure 121. Pachydactylus sansteynae (CAS 214589) from 1 km south of Huab River Bridge, Skeleton Coast National Park, Khorixas District, Namibia. Note the large head and the relatively pointed snout and the deep body profile. These are features shared with members of the Northwestern Pachydactylus clade, including $P$. gaiasensis and P. oreophilus. Photo courtesy of R.D. Babb.

Figure 122. Habitat of Pachydactilus sansternae in shales and other friable rocks near the Huab River Bridge. Skeleton Coast National Park, Khorixas District, Namibia. Photo by A.M. Bauer.


Diagnosis.- To 49.3 mm SVL (ZFMK 32925; Visser 1984 reported a maximum of 53.5 mm SVL but we examined no specimens in this size range). Pachydactylus serval may be distinguished from all other members of the $P$. serval/weberi group by the combination of the following characters: rostral enters nostril; supranasals in variable contact; scales on dorsum of head smooth and granular, those on snout larger than those of interorbital region; parietal scales tiny, granular, with no intermixed tubercles; dorsal scalation homogeneous, with only a few small, scattered flattened tubercles on sacrum and/or lumbar region; thighs without tubercles; toes relatively short with moderately wide pads; typically 5 undivided lamellae beneath digit IV of pes; tail to at least $107 \%$ SVL, moderately annulate, bearing whorls of small, rounded to pointed, unkeeled, white to yellow tubercles, widely separated form each other; adult pattern spotted (Figs. 2, 25-26), dark brown spots relatively large and arranged in more-or-less regular rows on a yellowish- to purplish-brown background, no nape band or nape band weakly evident; in some subadults adult spotted pattern and juvenile banding may cooccur (Fig. 27); juvenile pattern of a light (white to ashy) nape band and a similar broad band across posterior abdomen and sacrum and extending on to hindlimbs (although typically becoming more brownish or blackish distally on limbs), remainder of body dark, blackish in life (Figs. 28-29; see also Visser 1984:51), tail brownish.

Distribution.- Pachydactylus serval is a strictly Namibian endemic. Visser (1984) considered this form to range southward only as far as Bethanien and Aus. Griffin (2003) considered $P$. serval as limited to central Namibia, from Mariental to Keetmanshoop. Its core area of distribution is in central southern Namibia, but it has a more extensive distribution - from Mariental in the north to the Orange River in the south (Figs. 21, 30-31). Most records are from localities around 1500 m in the highland area stretching from the Tsarisberge and Schwarzrand south to the Huib Hochplateau and in areas bordering the Fish River. Outlying eastern localities include Daweb-Süd, Farm Florida in the Karasberge, and east of Keetmanshoop, whereas in the southwest, there is a single record north of Rosh Pinah. A record from near Swakopmund needs further investigation; on the basis of the habitat in this region and the disjunction from the contiguous portion of the range, we regard it as erroneous. However, the record is relatively recent and fairly precise and may represent an accidental translocation. Other localities of interest are along the Orange River and thus in sympatry or near sympatry with P. purcelli, P. montanus and a new species from the Richtersveld. One of these localities is between Noordoewer and Ai-Ais; this specimen appears to be unquestionably referable to $P$. serval, and specimens from relatively nearby (Ai-Ais) are clearly genetically distinct from any of these other species. A juvenile specimen (TM 36782) from the Farm Koboop (see Fig. 30) on the south bank of the Orange River, south of Onseepkans (2819Cd) has been tentatively referred to $P$. serval, but further investigation of this locality is required. Specimens here referred to $P$. montanus and $P$. purcelli have also been collected at this site.

Natural History. - Pachydactylus serval is typically found under exfoliating flakes or in narrow crevices in a variety of rock types. Road embankments (Fig. 32), borders of dry riverbeds, low exposures on ridge tops and cliff faces are all occupied if suitable retreats are present.

Visser (1984) reported that young near Bethanie hatch in mid-January and that egg size is $10.0-10.5 \times 6.6-7.4 \mathrm{~mm}$, with hatchlings measuring $19.2-22.6 \mathrm{~mm}$ SVL.

Conservation Status.- Pachydactylus serval is patchily distributed and although infrequently encountered in comparison to some other members of the $P$. serval group, it is locally common and under no specific threats. It is protected in the north of its range in the Hardap Recreation Resort and in the south in the Ai-Ais/Richtersveld Transfrontier Park. Griffin (2003) also indicated that it occurs in the Naute Recreation Resort.

Remarks.- Monard $(1931,1937)$ reported P. serval from from the Mbalé Stream, Indungu and Kuluï in Angola, where it was found under fallen trees. It seems likely that he was in fact refer-
ing to $P$. punctatus, which also has a spotted dorsum, and is one of relatively few Pachydactylus to occur in Angola.

The precise type locality of Pachydactylus serval has remained in doubt, as it is difficult as a result of years of farm consolidations and subdivisions to determine exactly where the Farm Chamis of 1910 is located today. At the suggestion of Mike Griffin (Ministry of Environment and Tourism, Windhoek), we visited the region near the present farm Chamis Süd and attempted to find the vantage point from which a panaoramic photo of the area near Chamis was taken in about 1905 (Schultze 1907). Based on our observations along the main (C14) road from Helmeringhausen to Bethanie, the closest match to this photo is the vista at a point approximately 10.1 km southeast of Helmeringhausen ( $25^{\circ} 56^{\prime} 56^{\prime \prime} \mathrm{S}, 16^{\circ} 53^{\prime} 50^{\prime \prime} \mathrm{E}$, elevation 1375 m ) on the Farm Goais (Fig. 32). However, the photo was taken on the Konkiep River itself, east of the existing main road. In all likelihood the precise location of Schultze's (1907) vantage point was on the existing farm Coruna at a point just north of the boundary with the farm Mooifontein. Although the type specimens could have been collected anywhere in the vicinity, we regard this locality, in QDS 2516Dd as the site of Werner's (1910) "Chamis."

Loveridge (1947) incorrectly stated that the juvenile pattern of this species was characterized by three cross bands.

## Pachydactylus purcelli Boulenger, 1910

Figures 4, 33-41.
1910 P[achydactylus]. purcelli Boulenger, Ann. S. Afr. Mus. 5: 494 (Syntypes: SAM 1260-61 (Fig. 33):
"Touw's River," coll. W.F. Purcell. SAM [not located]: "Little Namaqualand," coll. Schlechter. See Remarks regarding restriction of type locality. The description mentions several specimens from each locality, but we did not locate the Little Namaqualand types during a March 2005 visit to the South African Museum).
1911 P[achydactylus]. Purcelli Sternfeld, Mitt. Zool. Mus. Berlin 5:398.
1911 Pachydactylus pardus Sternfeld, Mitt. Zool. Mus. Berlin 5:398. (Holotype: ZMB 23453 (Fig. 34):
"Warmbad [Deutsch Sudwest-Afrika]" [Namibia]; coll. Schmidt).
1911 P[achydactylus]. purcelli Hewitt, Ann. Transvaal Mus. 3:45.
1913 [Pachydactylus] pardus Hewitt, Ann. Natal Mus. 2:483.
1913 [Pachydactylus] purcelli Hewitt, Ann. Natal Mus. 2:483.
1914 P[achydactylus] purcelli [part] Methuen and Hewitt, Ann. Transvaal Mus. 4:131, fig. 15 [part] (Fig. 4 [part]).
1927 [Pachydactylus] purcelli Hewitt, Rec. Albany Mus. 3:397.
1929 Pachydactylus pardus Lawrence, J. S.W. Afr. Sci. Soc. 2:25.
1935 [Pachydactylus] purcelli Hewitt, Rec. Albany Mus. 4:320.
1936 Pachydactylus purcelli Lawrence, Parasitology 28:38.
1935 Pachydactylus purcelli [part] FitzSimons, Ann. Transvaal Mus. 15:529.
1938 Pachydactylus purcelli FitzSimons, Ann. Transvaal Mus. 19:176.
1941 Pachydactylus purcelli FitzSimons, Ann. Transvaal Mus. 20:359.
1943 Pachydactylus purcelli [part] FitzSimons, Mem. Transvaal Mus. 1:65, pl. VIII, fig. 3, Pl. XIII, fig. 5.
1947 Pachydactylus purcelli Loveridge, Bull. Mus. Comp. Zool. 98:362.
1951 Pachydactylus purcelli Lawrence, Ann. Transvaal Mus. 21:452.
1955 Pachydactylus purcelli Mertens, Abhandl. Senckenberg. naturf. Ges. 490:48.
1965 Pachydactylus purcelli Wermuth, Das Tierreich 80:122.
1966 Pachydactylus [serval] purcelli McLachlan and Spence, Ann. Cape Prov. Mus. 5:155.
1971 Pachydactylus serval purcelli Mertens, Abhandl. Senckenberg. naturf. Ges. 529:42.
1981 Pachydactylus serval purcelli Branch, Ann. Cape Prov. Mus. (Nat. Hist.) 13:145.
1982 Pachydactylus serval purcelli Welch, Herpetology of Africa:36.

1984 Pachydactylus serval purcelli Visser, Landbouweekbl., 27 April 1984:48, fig. p. 49, second from bottom. 1988 Pachydactylus s. purcelli Branch, Field Guide:207, pl. 86, top.
1990 P[achydactylus]. serval purcelli Branch, J. Herpetol. Assoc. Afr. 37:25.
1991 [Pachydactylus] serval purcelli Kluge, Smithson. Herpetol. Inform. Serv. 85:23.
1991 Pachydactylus purcelli Bauer and Günther, Mitt. Zool. Mus. Berlin 67:294.
1991 Pachydactylus serval purcelli Bauer, J. Herpetol. Assoc. Afr. 39:18.
1993 [Pachydactylus] serval purcelli Kluge, Gekkonoid Lizard Taxonomy:25.
1994 Pachydactylus serval purcelli Welch, Lizards of the World 1:95.
1994 Pachydactylus s. purcelli Branch, Field Guide, 2nd ed.:207, pl. 86, top.
1995 Pachydactylus serval purcelli Branch and Bauer, Herpetol. Nat. Hist. 3:57.
1998 Pachydactylus s. purcelli Branch, Field Guide, $2^{\text {nd }}$ ed.:260, pl. 86, top.
2000 [Pachydactylus] serval purcelli Rösler, Gekkota 2:99.
2001 [Pachydactylus] serval purcelli Kluge, Hamadryad 26:21.
2003 Pachydactylus serval purcelli Griffin, Namibian Reptiles:38.
2005 P[achydactylus]. serval [part] Bauer and Lamb, Afr. J. Herpetol. 54:116.
Material examined.- South Africa: Western Cape Province: PEM R 7081-83, 6.8 km NE Eierspoort on Anysberg Rd. ( $33^{\circ} 37^{\prime} \mathrm{S}, 20^{\circ} 37^{\prime} \mathrm{E}$ ); CAS $180387-89,2 \mathrm{~km}$ W entrance Anysberg Reserve $\left(33^{\circ} 44^{\prime} \mathrm{S}, 20^{\circ} 27^{\prime} \mathrm{E}\right)$; PEM R 6721, 7010, Anysberg Nature Reserve, Voorsteberg (3320Bc; $33^{\circ} 27^{\prime} 13^{\prime \prime} \mathrm{S}$, $20^{\circ} 35^{\prime} 08^{\prime \prime} \mathrm{E}$ ); PEM R 8553, NW Anysberg to Ladismith ( $33^{\circ} 28^{\prime} 02^{\prime \prime} \mathrm{S}, 20^{\circ} 54^{\prime} 23^{\prime \prime} \mathrm{E}$ ); JDV 1522-24, 1527-28, 1533, 39078, SAM 7689, 44665. Matjiesfontein (3320Ba): TM 19505, 19552-54, 19579-80, 19582-83, Matjiesfontein ( $33^{\circ} 14^{\prime} \mathrm{S}, 20^{\circ} 35^{\prime} \mathrm{E}$ ); IRSNB 11820 (formerly TM 31284), TM $31280-83,31285-88,2 \mathrm{mi}$ N Matjiesfontein ( $33^{\circ} 12^{\prime} \mathrm{S}, 20^{\circ} 35^{\prime} \mathrm{E}$ );TM 34997-35001. 5 mi N Matjiesfontein ( $33^{\circ} 09^{\prime} \mathrm{S}, 20^{\circ} 35^{\prime} \mathrm{E}$ ); CAS $175278,60.9 \mathrm{~km}$ S Laingsburg on Hwy. 323 ( $33^{\circ} 29^{\prime} \mathrm{S}, 20^{\circ} 55^{\prime} \mathrm{E}$ ); TM 66083, nr. Plathuis turnoff, Ladismith Dist. ( $33^{\circ} 42^{\prime} \mathrm{S}, 20^{\circ} 52^{\prime} \mathrm{E}$ ): PEM R 7108; 8.6 km dirt rd. to Touwsrivier, Ladismith, Barrydale ( $33^{\circ} 38^{\prime} \mathrm{S}$, $20^{\circ} 58^{\prime}$ E); PEM R 8559, Farm Plathuis, S slopes of Touwsberg ( $33^{\circ} 37^{\prime} 43^{\prime \prime} \mathrm{S}, 20^{\circ} 56^{\prime} 19^{\prime \prime}$ E); TM 56426-27, Farm Combrinkskraal 93 ( $33^{\circ} 01 \mathrm{~S}, 21^{\circ} 59^{\prime} \mathrm{E}$ ); USEC/H-5715, Prins Albert (3322Ac); PEM R 3693, 3707, N slopes of Droekloofberg ( $33^{\circ} 16^{\prime} \mathrm{S}$, $22^{\circ} 37^{\prime} \mathrm{E}$ ); USEC/H-1291, Kromrivier A ( $32^{\circ} 31^{\prime} 37^{\prime \prime} \mathrm{S}, 19^{\circ} 17^{\prime} 31^{\prime \prime}$ E); USEC-H1300 , Kromrivier B ( $32^{\circ} 32^{\prime} 13^{\prime \prime} \mathrm{S}, 19^{\circ} 19^{\prime} 09^{\prime \prime} \mathrm{E}$ ); USEC/H-1278, Varkkloof, Grootrivier ( $32^{\circ} 38^{\prime} 09^{\prime \prime} \mathrm{S}$, $19^{\circ} 23^{\prime} 48^{\prime \prime} \mathrm{E}$ ); USEC/H-1195, Sonderwater, De Meul ( $32^{\circ} 47^{\prime} 00^{\prime \prime} \mathrm{S}, 19^{\circ} 27^{\prime} 37^{\prime \prime}$ E); USEC/H-1184-85, Zuurvlakte ( $32^{\circ} 46^{\prime} 47^{\prime \prime} \mathrm{S}, 19^{\circ} 29^{\prime} 48^{\prime \prime}$ ); USEC/H-1179, Ceres District, Skurweberg ( $32^{\circ} 45^{\prime} 52^{\prime \prime} \mathrm{S}, 19^{\circ} 26^{\prime} 15^{\prime \prime} \mathrm{E}$ ); JDV 7627-28, Farm Slagterhoek, 20 km N Prince Albert (3322Aa); USEC/H-2880, Botterkraal, Prins Albert District ( $33^{\circ} 06^{\prime}$ S, $22^{\circ} 25^{\prime}$ E); PEM R 4500-03, 4673, Bruinrante (3322Ba); PEM R 3707, Kammanasieberg, Elandsvlakte (3322Db); CAS 198294*-96*, Oukloof Pass, Farm Oukloof ( $32^{\circ} 11^{\prime} 36^{\prime \prime} \mathrm{S}, 21^{\circ} 55^{\prime} 38^{\prime \prime} \mathrm{E}$ ); USEC/H-2879. Prins Albert Road ( $32^{\circ} 57^{\prime} \mathrm{S}, 21^{\circ} 39^{\prime}$ E); MCZ R 46812, just S Beaufort West (3222Bc); SAM 1247-48, TM 19468, 20369-70, 20372-78. Beaufort West ( $32^{\circ} 21^{\prime}$ S, $22^{\circ} 35^{\prime}$ E); PEM R 3162-63, 3266-69, 4533, 4664-65, Karoo National Park (3222Ba). Eastern Cape Province: PEM R 4526-28, 2 km W Farm Lustfontein. Reitbron Dist. (3323Aa): PEM R 4525, 10 km W Farm Lustfontein, Reitbron Dist. (3322Bb); PEM R 6506-10, 12 km W Vondeling Stn. ( $33^{\circ} 19^{\prime} \mathrm{S}, 22^{\circ} 57^{\prime} \mathrm{E}$ ); PEM R 4858-62, Farm Vleikop, Wolweboslaagte (3323Aa). Northern Cape Province: JDV 2136, 20 km S Sutherland (3220Da); SAM 43966, Middelpos ( 3120 Cd ); TM $35035-39,3 \mathrm{mi}$ W Middelpos ( $31^{\circ} 56^{\prime} \mathrm{S}, 20^{\circ} 21^{\prime} \mathrm{E}$ ); TM 35046-47, 9 mi SE Middelpos ( $31^{\circ} 59^{\prime} \mathrm{S}, 20^{\circ} 21^{\prime} \mathrm{E}$ ); TM 36156-59. Farm Gansvley ( $31^{\circ} 28^{\prime} \mathrm{S}, 21^{\circ} 58^{\prime} \mathrm{E}$ ); TM 36160, Farm Tabaksfontein ( $31^{\circ} 38^{\prime} \mathrm{S}, 21^{\circ} 48^{\prime} \mathrm{E}$ ); TM 36161-67. Farm Grootfontein, Fraserburg Dist. ( $31^{\circ} 50^{\prime} \mathrm{S}, 21^{\circ} 38^{\prime} \mathrm{E}$ ); TM 36231, Farm Grootkolk, Williston Dist. ( $31^{\circ} 06^{\prime} \mathrm{S}, 20^{\circ} 54^{\prime} \mathrm{E}$ ): TM 36174, 36188-90, 4 mi NE Fraserburg ( $31^{\circ} 50^{\prime} \mathrm{S}, 21^{\circ} 35^{\prime} \mathrm{E}$ ); TM 36182-87. Farm Bamburgershoogte, 6 mi SE Fraserburg ( $31^{\circ} 59^{\prime} \mathrm{S}, 21^{\circ} 34^{\prime} \mathrm{E}$ ); TM 36201-04. Farm Quaggasfontein, 10 mi N Fraserburg ( $31^{\circ} 50^{\prime} \mathrm{S}$, $21^{\circ} 27^{\prime} \mathrm{E}$ ); TM 36214-19, 36230, Farm Goedverwagting. Williston Dist. ( $31^{\circ} 50^{\prime} \mathrm{S}, 21^{\circ} 34^{\prime} \mathrm{E}$ ): CAS 199995, Williston Rd., 15 km NW Fraserburg ( $31^{\circ} 47^{\prime} 06^{\prime \prime} \mathrm{S} .21^{\circ} 25^{\prime} 05^{\prime \prime}$ E): PEM R 4775, 4780, 40 km N Williston (3120AD); TM 36249-50, Farm Bleskrans, Williston Dist. ( $30^{\circ} 55^{\prime} \mathrm{S}$, $20^{\circ} 36^{\prime} \mathrm{E}$ ): SAM 47723. Verneukpan (Suid) ( $30^{\circ} 06^{\prime} 31^{\prime \prime} \mathrm{S}, 21^{\circ} 02^{\prime} 13^{\prime \prime} \mathrm{E}$ ); TM $18218-24$, 18226-27, 18229-31, 39108. Van Wyk’s Vlei ( $30^{\circ} 21^{\prime}$ S, $21^{\circ} 49^{\prime}$ E); TM 18209-12, 18214, 18216-17, MCZ R 46811 (formerly TM 18213), 15 mi. from Van Wyk's Vlei (3021Bc); SAM 47715-16, Verdorskalk $\left(30^{\circ} 05^{\prime} 11^{\prime \prime} \mathrm{S}, 20^{\circ} 25^{\prime} 50^{\prime \prime}\right.$ E): SAM 47721-22. Kareeboomleegte ( $30^{\circ} 04^{\prime} 27^{\prime \prime} \mathrm{S}, 20^{\circ} 54^{\prime} 35^{\prime \prime} \mathrm{E}$ ); TM 62905 ,

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Carolusberg, Namaqualand ( $29^{\circ} 38^{\prime} \mathrm{S}, 17^{\circ} 57^{\prime} \mathrm{E}$ ) [locality questionable]; CAS 201843, 201844*, 201845-49, 203488-93, PEM R $12471^{*}, 12475^{*}, 28.3 \mathrm{~km}$ E Pofadder on Hwy. R64 ( $29^{\circ} 01^{\prime} 17^{\prime \prime} \mathrm{S}, 19^{\circ} 39^{\prime} 06^{\prime \prime}$ E); TM 28031-32 21 mi NE Pofadder towards Kakamas ( $29^{\circ} 01^{\prime} \mathrm{S}, 1^{\circ} 40^{\prime} \mathrm{E}$ ); JDV 2562-70, 34 km E Pofadder (2919Aa); JDV 2553-54, 2557, 26 km E Pofadder (2919Aa);TM 27628, Farm Rietfontein ( $29^{\circ} 25^{\prime} \mathrm{S}, 20^{\circ} 55^{\prime} \mathrm{E}$ ); JDV 5492-94, 61 km S Kenhardt (2920Dd); SAM 47718-19, Bloubos ( $29^{\circ} 56^{\prime} 32^{\prime \prime}$ S, $20^{\circ} 48^{\prime} 13^{\prime \prime}$ E); SAM +7720, Bloubos ( $29^{\circ} 55^{\prime} 14^{\prime \prime} \mathrm{S}, 20^{\circ} 57^{\prime} 07^{\prime \prime} \mathrm{E}$ ); TM 36732, Driekop, 8 km S Kenhardt ( $29^{\circ} 22^{\prime} \mathrm{S}, 21^{\circ} 06^{\prime} \mathrm{E}$ ); PEM (number pending), Kokerboomwoud, 8 km S Kenhardt ( $29^{\circ} 24^{\prime} 22 \mathrm{~S}^{\prime \prime}, 21^{\circ} 06^{\prime} 18^{\prime \prime}$ E); TM 28050, Farm Kaboom (2922Aa): TM 28053, Farm Witvlei, 25 mi . W Prieska (2922Cb); TM 15936, between Kenhardt and Prieska; TM 82319-21, 10 km from Duine Municipal Site (2821Ac); CAS 126035-37, 19 mi SW Upington on rd. to Keimoes (2821Ca); TM 28015, Farm Koboop (Coboboop) ( $28^{\circ} 53^{\prime} \mathrm{S}, 19^{\circ} 20^{\prime} \mathrm{E}$ ); PEM R 217, 60 mls . From Onseepkans E. (2820Cb); PEM R 128, 133, 146, 155, 160, 25 mls . N Pofadder (2819Cd); JDV 2539-40, 2551-52, 2555-56, 36 km E Pofadder (2819Dc); ZFMK 52394, 70 km E Pofadder (2819Dd); CAS 186277, 81 km E Namibian border on Upington-Ariamsvlei Rd. (2820Bd); NMNW R 121, TM 15912, 15921, Kakamas ( $28^{\circ} 45^{\prime} \mathrm{S}, 20^{\circ} 33^{\prime} \mathrm{E}$ ); TM 37593, Farm Rooidam, 11 km W Augrabies ( 2820 Cb ); SAM 17330 ( 2 specimens), Aughrabies Falls, N bank of river (2820Cd); TM 28040-41, 56195, Augrabies Falls Natl. Pk. (2853'S, $20^{\circ} 20^{\prime}$ E); SAM 3511-12, Naroep (2818Dc). Namibia: Karasburg District: JDV 2624, 20 km S Ariamsvlei (2819Bd); SAM 17016, Kalkfontein (2818Ba); PEM R 157, 180, TM 33289, ZMB 23453 (holotype of P. pardus), Warmbad (2818Bc); PEM R 121, 127, 159, 225, 16 mi . S Warmbad (2818Db); PEM R 214, $18 \mathrm{mi} . \mathrm{S}$ Warmbad ( 2818 Db ); TM $17855-56,15$ miles S Warmbad ( $28^{\circ} 37^{\prime} \mathrm{S}, 18^{\circ} 52^{\prime} \mathrm{E}$ ); TM 79077, Warmbad ( $28^{\circ} 26^{\prime} \mathrm{S}$, $18^{\circ} 44^{\prime} \mathrm{E}$ ); CAS 231887, Farm Narudas, 7 km N of Road D201 ( $27^{\circ} 23^{\prime} 09^{\prime \prime} \mathrm{S}, 18^{\circ} 52^{\prime} 26^{\prime \prime} \mathrm{E}$ ); Keetmanshoop District: PEM R 104-06, 108-115, 14561 (formerly AM 3089), Kraikluft (2718Ba); NMNW R 122, TM 3088, Alt Wasserfall ( $27^{\circ} 08^{\prime}$ S, $18^{\circ} 39^{\prime}$ E); PEM R 126, 158, 220, Kochena ( 2718 Bb ); TM 3102-03, between Kraikluft and Alt Wasserfall (2718Ba). Unidentifiable/ambiguous locality: SAM 3496, Kraaifontein, Namaqualand. Unknown locality: JDV 767. Additional literature record: South Africa: Western Cape Province: Karoo National Park (as P. serval; Girard 1997).

Diagnosis.- To 50.8 mm SVL (CAS 231887). Pachydactylus purcelli may be distinguished from all other members of the $P$. serval/weberi group by the combination of the following characters: head blunt, wide; rostral enters nostril; supranasals usually in broad anterior contact; scales on dorsum of head smooth and flattend, often polygonal rather than rounded, those on snout only slightly larger than those of interorbital region; dorsal scalation homogeneous, no tubercles on dorsum of body or thighs; toes moderately long and narrow with moderately wide pads; typically 5 undivided lamellae beneath digit IV of pes; tail to at least $120 \%$ SVL, moderately annulate, bearing whorls of very small, flattened, unkeeled, well-separated, white to yellow tubercles; adult pattern buff to beige or pastel yellow, orange or purple with small, irregular, closely-spaced brown spots covering entire dorsum and flanks, remnants of three pale (white, yellow or purplish-gray) cross bands may be retained in some adults, especially in northern populations (Figs. 35-38); juvenile pattern with three light (white to yellow) cross bands: one on nape, one on trunk and one over or just anterior to sacrum - that on nape often extended posteriorly along midline (Figs. 39-41).

Distribution.- Widely distributed in the western portions of the Great and Little Karoo of South Africa (Branch 1990; Branch and Bauer 1995) as far east as the western Eastern Cape Province, where it is the only member of the $P$. serval/weberi clade to occur. It occurs along the Orange River from the level of Upington to Warmbad. Its distribution in South Africa is largely complementary to that of $P$. weberi. A western locality, Carolusberg, is probably in error or perhaps represents an isolated population (Fig. 31, blue "?"). Pachydactylus purcelli extends into southeastern Namibia as far north as the Karasberg Mountains (e.g., Methuen and Hewitt 1914), although it is unclear if Namibian populations are continuously distributed or patchy (Figs. 21, 30-31). Griffin (2003) considered that most "serval" from southern Namibia (Karasburg, southern Bethanie and Lüderitz districts) were assignable to $P$. purcelli. Based on our studies, Karasburg records are based on both P. purcelli and P. montanus but $P$. purcelli does not occur further west in Namibia. Parker's
(1936) records of P. purcelli from Maltahöhe certainly refer to $P$. serval. Pachydactylus purcelli occurs in sympatry or near sympatry with $P$. montanus at Koboop on the south bank of the Orange and near Warmbad in Namibia. It occurs with both P. montanus and a new species of the serval group at Farm Narudas in the Karasberg. A record from Bechuanaland [Botswana] noted questioningly by Loveridge (1947) is clearly incorrect.

Natural History.- A rupicolous species which has been recorded from narrow cracks and under exfoliating flakes in shale, dolerite, Dwyka tillite, sandstone, and other outcrops in the Little Karoo (Branch 1990; Burger 1993; Branch and Bauer 1995) and in sandstone and dolerite, in particular, in the Great Karoo (Branch and Braack 1989; Haagner and Branch 1995; Fig. 42). In southeastern Namibia it appears to utilize similar retreats in rock crevices or under rock slabs (Fig. 43). FitzSimons (1943) reported some background color matching ability in this species. Lawrence (1951) described the parasitic mite Geckobia capensis hastata from P. purcelli.

Conservation Status. - Pachydactylus purcelli is widely distributed in western South Africa and is under no immediate threats. It is protected in the Karoo National Park, Anysberg Nature Reserve, and Swartberg Nature Reserve, and probably in the Sanbona Wildlife Reserve. Namibian populations do not occur in any parks or reserves but do not appear to be under threat.

Remarks.- Mertens (1955) restricted the type locality to "Townsriver [sic], Kap-Provinz." Pachydactylus pardus was synonymized with P. purcelli by Methuen and Hewitt (1914) and this interpretation was endorsed by FitzSimons (1938). The absence of tubercles in the holotype is consistent with this; however, there is extensive variation in this feature in P. montanus as well. We examined the holotype of $P$. pardus (Fig. 34), which is in moderately good condition, and concur that it is conspecific with P. purcelli. Methuen and Hewitt (1914) described the juvenile pattern of P. purcelli from the Karasburg as "dorsally five light transverse bars which have irregular dark edges." This pattern is, in fact, more consistent with that of P. montanus (the fifth band described by Methuen and Hewitt occurs on the tail base) and it is evident that their series was composite (Fig. 4).

We were unable to locate the "Little Namaqualand" syntypes in the collection of the South African Museum. Both M. Schlechter and F.R.R. Schlechter collected zoological and botanical specimens in Namaqualand around the turn of the century and it is unclear which was the collector cited by Boulenger (1910).

## Pachydactylus montanus Methuem and Hewitt, 1914

Figures 4, 44-51.
1914 P[achidactolus]. montanus Methuen and Hewitt, Anm. Transvaal Mus. 4:129 (Holotype: TM 3080 (Fig. 44): "Lord Hill's Peak in the Great Karas Mountains, at an altitude of 7300 feet," coll. P.A. Methuen, 17 January 1913).
1914 P[achydactylus] purcelli [part] Methuen and Hewitt Ann. Transvaal Mus. 4:131, fig. 15.
1927 [Pachydactylus] montanus Hewitt, Rec. Albany Mus. 3:395, pl. XXII, fig. 3.
1935 Pachydactylus montanus onscepensis Hewitt, Rec. Albany Mus. 4:318 (Holotype: PEM R 16050 (formerly AM 6879) (Fig. 45): Adult female; "Onscephans [= Onseepkans] on the Orange River, not far from Pella," coll. Dr. H. Maughan Brown).
1935 Pachydactylus purcelli [part] FitzSimons, Ann. Transvaal Mus. 15:529.
1936 Pachydactylus montanus Lawrence, Parasitology 28:38.
1938 Pachydactylus montanus onscepensis [part] FitzSimons, Ann. Transvaal Mus. 19:173.
1943 Pachydactylus purcelli [part] FitzSimons, Mem. Transvaal Mus. 1:65.
1943 Pachydactvlus montanus montanus FitzSimons, Mem. Transvaal Mus. 1:83.
1943 Pachisdacțlus montanus onscepensis [part] FitzSimons, Mem. Transvaal Mus. 1:84, pl. VIII, fig. 5, Pl. XV. fig. 3.

1947 Pachydactylus serval [part] Loveridge, Bull. Mus. Comp. Zool. 98:388.<br>1955 Pachydactylus serval [part] Mertens, Abhandl. Senckenberg. naturf. Ges. 490:48.<br>1965 Pachydactylus serval [part] Wermuth, Das Tierreich 80:123.<br>1966 [Pachydactylus serval] onscepensis [part] McLachlan and Spence, Ann. Cape Prov. Mus. 5:155.<br>1966 [Pachydactylus serval] serval [part] McLachlan and Spence, Ann. Cape Prov. Mus. 5:155.<br>1971 Pachydactylus serval serval [part] Mertens, Abhandl. Senckenberg. naturf. Ges. 529:42.<br>1981 Pachydactylus serval onscepensis [part] Branch, Ann. Cape Prov. Mus. (Nat. Hist.) 13:145.<br>1982 Pachydactylus serval serval [part] Welch, Herpetology of Africa:36.<br>1982 Pachydactylus serval onscepensis Welch, Herpetology of Africa:36.<br>1984 Pachydactylus serval serval [part] Visser, Lanbouweekbl. 27 April 1984:48, fig. p. 48, top.<br>1984 Pachydactylus serval onscepensis Visser, Lanbouweekbl. 27 April 1984:48, fig. p. 51, top.<br>1988 Pachydactylus s. onscepensis [part] Branch, Field Guide:207, pl. 86, upper middle left.<br>1991 [Pachydactylus] serval onscepensis Kluge, Smithson. Herpetol. Inform. Serv. 85:24.<br>1993 [Pachydactylus] serval onscepensis Kluge, Gekkonoid Lizard Taxonomy:25.<br>1994 Pachydactylus serval onscepensis Welch, Lizards of the World 1:95.<br>1994 Pachydactylus s. onscepensis [part] Branch, Field Guide, $2^{\text {nd }}$ ed.:207, pl. 86, upper middle left.<br>1996 Pachydactylus weberi ex errore Branch, Afr. Herp News 25:27.<br>1998 Pachydactilus s. onscepensis [part] Branch, Field Guide, $3^{\text {rd }}$ ed.:260, pl. 86, upper middle left.<br>2000 [Pachydactylus] serval onscepensis Rösler, Gekkota 2:99.<br>2001 [Pachydactylus] serval onscepensis Kluge, Hamadryad 26:21.<br>2003 Pachydactylus serval onscepensis Griffin, Namibian Reptiles:38.<br>2005 P[achydactylus]. serval [part] Bauer and Lamb, Afr. J. Herpetol. 54:116.

Material examined.- South Africa: Northern Cape Province: JDV N26180, 100 km N Wallekraal ( 2917 Ca )[locality questionable]; PEM R $119,123,18 \mathrm{mi}$. from Goodhouse on Pofaddder Rd. (2918Ab); TM 27654, 11 km SE Farm Aggenys (2918Bb); TM 15365, 15643-44, Pofadder (2919Ab); JDV N23580. 29 km S Onseepkans (2919Ab); TM 27634-39, 27644-46, Farm Olyvenkolk ( $29^{\circ} 26^{\prime} \mathrm{S}, 2^{\circ}{ }^{\circ} 52^{\prime} \mathrm{E}$ ); JDV 1929, 2035, 97 km E Octa Diamond Mine (2817Ab); CAS 167647, 10 km S Vioolsdrif on Hwy. N7 (2817Dc); SAM 46726-28, 8 km SE Vioolsdrif (2817Dc); SAM 43682, Vioolsdrif (2817Dc); TM 17864, Goodhouse ( $28^{\circ} 54^{\prime}$ S, $18^{\circ} 14^{\prime}$ E); JDV 1180-81, S outskirts of Goodhouse ( 2818 Cc ); TM 28016, Farm Koboop (Coboboop) (2819Cd); PEM R 120, 122, 221, 223, Mt. Stofel (2818Cc); JDV N20380, 47 km S Ariamsvlei (2819Bc); PEM R 16050 [formerly AM 6879, holotype of $P$. montanus onscepensis], PEM R 2390, 2476-78, CAS 231883-85*, Onseepkans ( 2819 Cb ); TM 15645, Onseepkans ( $28^{\circ} 44^{\prime}$ S, $19^{\circ} 17^{\prime} \mathrm{E}$ ); CAS 201859*-60*, 203498*, PEM R $12516^{*}-17$, 5.0 km S Onseepkans on Hwy. R358 ( $28^{\circ} 47^{\prime}$ i $7^{\prime \prime}$ S, $19^{\circ} 19^{\prime} 31^{\prime \prime}$ E); PEM R 124, 141, 218, 20 mi from Onseepkans E. (2819Cb); SAM 17376, Baks Putz (Bak-se-puts), Gordonia (2820Ac); PEM R 125, 148, 219, 60 mi. from Onseepkans E (2820Cc); TM 36754-58, Farm Schuitdrif on Orange River (2819Da); TM 68557, Riemvasmaak ( $28^{\circ} 27^{\prime} \mathrm{S}, 20^{\circ} 19^{\prime} \mathrm{E}$ ); TM 28042, CAS 126046, Augrabies Falls (2820Cb); JDV 34579, Aughrabies ( 2820 Cb ); TM 56194, Augrabies National Park ( $28^{\circ} 35^{\prime} \mathrm{S}$, $20^{\circ} 20^{\prime}$ E); PEM R $5775 *-76$, at entrance to Augrabies Falls National Park ( 2820 Cb ); PEM R 5774*, 6 km from Blouputs Rd. on Blouputs Approach Rd. (2820Ca); IRSNB 11817 (formerly TM 15190), PEM R 16051 [formerly AM 2593], MCZ R 41853-54, TM 15909, 15911, 15913, 15915-17, 15920, 15922, Kakamas ( $28^{\circ} 45^{\prime}$ 'S, $20^{\circ} 33^{\prime}$ E); CAS 176256*-58*, Kenhardt Rd., ca. 18 km SE Kakamas (2820Dc); TM 36768-69, Farm Onder Swartmodder ( $28^{\circ} 43^{\prime} \mathrm{S}, 19^{\circ} 42^{\prime} \mathrm{E}$ ). Namibia: Lüderitz District: CAS 201892, NMNW R 8874*-75*, Witputz Annex (85), ca. 50 km N Rosh Pinah ( $27^{\circ} 39^{\prime} 33^{\prime \prime} \mathrm{S}$, $16^{\circ} 47^{\prime} 38^{\prime \prime} \mathrm{E}$ ); JDV 1905, btwn Ochta Mine and Rosh Pinah ( 2816 Bb ); CM 115705, 30 km E Aus (2616Da); Bethanie District: JDV 1819, 31380, Farm Houmoed (2616Ba); Karasburg District: NMNW R 10490, Noordoewer ( $28^{\circ} 39^{\prime} 48^{\prime \prime} \mathrm{S}, 17^{\circ} 49^{\prime} 23^{\prime \prime} \mathrm{E}$ ); NMNW R 10491-92, Haib Mine ( $28^{\circ} 41^{\prime} 49^{\prime \prime} \mathrm{S}, 17^{\circ} 53^{\prime} 26^{\prime \prime} \mathrm{E}$ ); JDV 34780, Noordoewer-Ai-Ais turnoff (2817Bd); PEM R 143, 5 mi . N Onseepkans (2819Cb); TM 28011-13, 13 km N Onseepkans (2819Cb); JDV N12980, 56 km N Onseepkans (2819Ac); PEM R 9290, Farm Velloor ( $28^{\circ} 35^{\prime}$ S, $19^{\circ} 12^{\prime}$ E); CAS 175320, 77.1 km E Karasburg on Hwy. B3 (2819Ba); SAM 46721-23, Norachaskop (2818Aa); CAS 201861, 3.5 km N Tantalite Valley, 12 km SW jct. Warmbad Rd. ( $28^{\circ} 42^{\prime} 08^{\prime \prime} \mathrm{S}, 18^{\circ} 47^{\prime} 33^{\prime \prime}$ E); TM 33289, Warmbad ( 2818 Bc ); TM 17855-56, Farm Lugeck ( $28^{\circ} 37^{\prime}$ S, $18^{\circ} 52^{\prime}$ E); CAS 201864*, PEM R 12522, Farm Kinderzitt ( $28^{\circ} 39^{\prime} 34^{\prime \prime}$ S, $18^{\circ} 41^{\prime} 47^{\prime \prime}$ E); CAS 201865*,

Farm Haakiesdoorn ( $28^{\circ} 51^{\prime} 44^{\prime \prime} \mathrm{S}, 18^{\circ} 14^{\prime} 38^{\prime \prime} \mathrm{E}$ ); PEM R 12526, N end Goodhouse'se poort, Farm Haakiesdoorn ( $28^{\circ} 44^{\prime} 47^{\prime \prime} \mathrm{S}, 18^{\circ} 17^{\prime} 02^{\prime \prime} \mathrm{E}$ ); CAS 201867*, NMNW R 8846*, Farm Witputs ( $28^{\circ} 28^{\prime} 24^{\prime \prime} \mathrm{S}$, $17^{\circ} 57^{\prime} 53^{\prime \prime} \mathrm{E}$ ); NMNW R 8832*-33*, Farm Umeis ( $28^{\circ} 42^{\prime} 08^{\prime \prime} \mathrm{S}, 18^{\circ} 47^{\prime} 33^{\prime \prime} \mathrm{E}$ ); TM 54733-34, Farm Sperlingsputs 259 ( $28^{\circ} 43^{\prime} \mathrm{S}$, $18^{\circ} 13^{\prime} \mathrm{E}$ ); NMNW R 8841*, Farm Ramanspoort ( $28^{\circ} 47^{\prime} 23^{\prime \prime} \mathrm{S}$, $18^{\circ} 23^{\prime} 55^{\prime \prime} \mathrm{E}$ ); CAS 201870, PEM R 12527, Farm Witputs ( $28^{\circ} 36^{\prime} 29^{\prime \prime}$ S, $17^{\circ} 59^{\prime} 53^{\prime \prime}$ E); TM 36807-09, Farm Eendoorn ( $28^{\circ} 42^{\prime}$ S, $18^{\circ} 57^{\prime}$ E); JDV 2620, 20 km S Ariamsvlei (2819Bb); CAS 201876, Ai-Ais Nature Reserve, 82.4 km W Noordoewer ( $28^{\circ} 11^{\prime} 07^{\prime \prime}$ S, $17^{\circ} 14^{\prime} 58^{\prime \prime}$ ) ; TM 45786 ( 2 specimens), between Grünau and Noordoewer (2818Aa); TM 41873-80, Confluence Kanebis and Fish Rivers, Farm Fish River Canyon 381 ( $27^{\circ} 46^{\prime}$ S, $17^{\circ} 36^{\prime}$ E); CAS 167648-49, 8.3 km W of Hwy. 324 turnoff on Hwy. 97 (2717Dc); CAS 176252*, 176253, 176254*-55*, 7 km N Grabwasser on Hwy. C12 (2718Ca); CM 119306-07, 79.5 km S Keetmanshoop on Rte. B1 (2718Ba); JDV 30880, 35080(2), 35480, btwn Grünau and Klein Karas (2718Ca); JDV 1922-24, 1926(2), 14 km W Grünau (2718Cb); ZMB 54387-88, Grünau (2718Cb); PEM R 134, 138, 142, 10 mi. W. Grünau (2718Cc); Keetmanshoop District: JDV 31580, Holoog (2718Ac); TM 17841, Farm Kochena ( $27^{\circ} 03^{\prime}$ S, $18^{\circ} 50^{\prime} \mathrm{E}$ ); TM 3080 (holotype of P. montanus), Lord Hill's Peak, Great Karas Mountains (2718Ba); SAM 46446, 46452-54, 46468-71, Kraikluft (2718Ba); TM 3089-96, Farm Pieterskloof, Kraikluft ( $27^{\circ} 14^{\prime}$ S, $18^{\circ} 45^{\prime}$ E); CAS 126058-59, 23 mi N Grünau (2718Ad); CAS 175321-24, Hwy. 203, 39.1 km SE of Hwy. B1 (2718Bc); SAM 46711, 46717-19, 46732-33, Farm Goibib (2718Bc); PEM R107, SAM 46714-16, Dassiefontein (2718Bc); AMB (MCZ Field) A38332-41, Savanna Guest Farm ( $27^{\circ} 23^{\prime} 10^{\prime \prime} \mathrm{S}, 18^{\circ} 29^{\prime} 30^{\prime \prime} \mathrm{E}$ ); AMB (MCZ Field) A38368-70, Savanna Guest Farm ( $27^{\circ} 22^{\prime} 56^{\prime \prime} \mathrm{S}, 18^{\circ} 28^{\prime} 30^{\prime}$ E); AMB (MCZ Field) A38375-78, Savanna Guest Farm ( $27^{\circ} 22^{\prime} 32^{\prime \prime}$ S, $18^{\circ} 29^{\prime} 33^{\prime \prime}$ E); SAM 46720, Noachabeb (2718Bc); CAS $214530,35.0 \mathrm{~km}$ E Keetmanshoop on Aroab Rd. ( $26^{\circ} 36^{\prime} 17^{\prime \prime} \mathrm{S}, 18^{\circ} 28^{\prime} 15^{\prime \prime}$ E); SAM 46708, 46729-30, 10 km N Keetmanshoop (2618Ac); TM 41936, 41938-40, 15 km N Keetmanshoop (2618Ac); SAM 46701-05, 20 km N Keetmanshoop (2618Ac); JDV 31680, 31780, 31880, 31980, 32080, 32180, 32480, 33980, 34080, between Narubis and Aroab (2618D or 2619C or 2619D); JDV N40180, Keetmanshoop (2618CA).

Diagnosis.- A small species, to 43.3 mm SVL (JDV 1923). Pachydactylus montanus may be distinguished from all other members of the $P$. serval/weberi group by the combination of the following characters: rostral enters nostril; supranasals in variable contact; scales on dorsum of head smooth, flattened to domed, those on snout much larger than those of interorbital region; scales of parietal region granular, homogeneous or with scattered conical tubercles scarcely larger than granules; dorsal scalation variable from nearly homogeneous to moderately heterogeneous, ranging from a few, small granular to flattened tubercles on sacrum, to slightly enlarged scattered tubercles on flanks and sacrum, to $10-12$ regularly arranged rows of flattened, conical, or keeled tubercles across dorsum and flanks; toes moderately long with moderately wide pads; typically 5 undivided lamellae beneath digit IV of pes; tail to at least $115 \%$ SVL, moderately annulate, bearing whorls of relatively large, pointed, smooth to weakly keeled, well-separated, white to pale yellow tubercles; adult pattern buff, yellowish-brown or pinkish or purplish-gray with relatively large brown spots and/or cross bands, often retaining evidence of juvenile dark band edges (Figs. 46-49); juvenile pattern of four dark-edged light (cream, buff, or yellowish brown) bands: nape, immediately behind axilla, mid-trunk, and presacral (Figs. 50-51; see also Visser (1984:51).

Distribution.-Mertens (1971) considered Pachydactylus montanus as limited to South Africa based on data presented by McLachlan and Spence (1966). Visser (1984) and Griffin (2003), however, believed that it occurred on both sides of the Lower Orange River Valley. It is distributed along both banks of the Orange River from approximately Kakamas to Vioolsdrif. In Namibia it also occupies the area east of the Fish River, including the western and northern Karasberg Mountains, as far north as Keetmanshoop (Figs. 21, 30-31). There are also several localities in the Lüderitz District north of Rosh Pinah and many specimens from a far southeastern locality, Farm Olyvenkolk, near Kenhardt. A specimen from 30 km east of Aus (CM 115705) is tentatively referred to this species as is a disjunct record from Farm Houmoed in the Tirasberge. The former record is consistent with Visser`s (1984) locality east of Aus. Despite their isolation, these records
appear to be valid, but one from north of Wallekraal, south of Anenous Pass in the western Northern Cape (Fig. 31, yellow "?") needs verification. Pachydactylus montanus occurs in sympatry or near sympatry with $P$. purcelli at several localities on the Orange River from Onseepkans upstream and in the Great Karasberg, with $P$. serval in the Bethanie District and near Noordoewer, and with a new serval group species at several localities between Goodhouse and Rosh Pinah.

The collection of the type of $P$. montanus at $7300 \mathrm{ft}(2225 \mathrm{~m})$ means that this species has the greatest elevational range of any member of the group, from near sea level in the Orange River Valley to the highest point of the Great Karasberg Mountains.

Natural History. - This species is variable in its use of habitat, but is always associated with rock crevices (Methuen and Hewitt 1914) or with rock flakes (Figs. 52-53).

Conservation Status.- Pachydactylus montanus occurs in the Ai-Ais/Richtersveld Transfrontier Park. It is locally abundant, especially along the Orange River, but is patchy in its distribution. It is under some threat because of the intensive agricultural use of portions of the Orange River Valley, but north of the river in Namibia it is subject to minimal human activity.

Remarks.- The description of Methuen and Hewitt (1914) provides sufficient information to identify $P$. montanus as specifically identical with $P$. onscepensis among the taxa recognized here and this has been confirmed by examination of the types associated with both names (Figs. 44-45). The dating of the paper by Methuen and Hewitt has been discussed by van Dijk (1996) and Branch (1996).

Loveridge (1947) synonymized both $P$. montanus and $P$. m. onscepensis with $P$. serval. Subsequent authors (Table 1) resurrected the latter from synonymy, but did not address the status of $P$. montanus, or accepted Loveridge's allocation of the unique specimen to $P$. serval. Although $P$. montanus has temporal priority over P. onscepensis, it has not been used as valid since 1947. The younger name, chiefly as a subspecies of $P$. serval, has been employed by numerous modern authors (Table 1). However, Article 23.9 of The International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999) provides for the automatic reversal of temporal precedence only when 1) "the senior synonym or homonym has not been used as a valid name after 1899" (Art. 23.9.1.1) and 2) "the junior synonym or homonym has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years" (Art. 23.9.1.2). Although the second provision is almost certainly fulfilled, the first is clearly not. Although the ICZN could be petitioned to use its plenary powers to set aside the older name, we see no compelling case for this as the name onscepensis has appeared chiefly in checklists or general faunal accounts and existing usage is not substantially disrupted by its abandonment in favor of P. montanus.

Hewitt (1927) considered $P$. montanus to be allied to $P$. scutatus. The variability of this taxon with respect to dorsal tuberculation was first alluded to by Hewitt (1935), who had difficulty assigning a specimen from Kakamas, which was weakly tuberculate. This species has remained perhaps the most problematic of all Pachydactylus. FitzSimons (1943) incorrectly stated that the juvenile color pattern of this species was almost indistinguishable from that of $P$. purcelli. In fact the juvenile color pattern of this species (Fig. 51) is unambiguously diagnostic, and many adults may also be identified on the basis of color alone. However, faded adult specimens from the Karasburg Region or from the adjacent Northern Cape may be difficult to distinguish from P. purcelli, and specimens from the Keetmanshoop district may be confused with $P$. serval. This species exhibits extensive genetic variation. Populations from Onseepkans are highly divergent from all others, forming the sister group to the remaining representatives of montanus in the Bayesian tree. Although genetic substructuring is apparent within the remainder of the montanus clade, it does not
appear to correspond to any obvious geographic pattern (see Phylogenetic Relationships). This taxon would be an ideal candidate for a more extensive phylogeographic analysis.

## Pachydactylus werneri Hewitt, 1935

Figures 54-57.
1935 Pachydactylus capensis werneri Hewitt, Rec. Albany Mus. 4:315, pl. XXIX, fig. 3 (Lectotype [here designated, see Remarks]: PEM R 16049 (formerly AM 6613 [part]) (Fig. 54): "Khan River, South West Africa," coll. R. D. Bradfield. Paralectotype: PEM R16048 (formerly AM 6613 [part]): same collection data as lectotype. Stuart (1980) mistakenly referred to a single type).
1935 [Pachydactylus capensis] weberi Hewitt, Rec. Albany Mus. 4:315.
1935 [Pachydactylus capensis] gariesensis Hewitt, Rec. Albany Mus. 4:315.
1943 Pachydactylus werneri FitzSimons, Mem. Transvaal Mus. 1:85
1947 Pachydactylus weberi werneri [part] Loveridge, Bull. Mus. Comp. Zool. 98:394.
1955 Pachydactylus werneri Mertens, Abhandl. Senckenberg. naturf. Ges. 490:49, fig. 108.
1965 Pachydactylus werneri Wermuth, Das Tierreich 80:124.
1971 Pachydactylus werneri Mertens, Abhandl. Senckenberg. naturf. Ges. 529:43.
1980 Pachydactylus weberi werneri Stuart, J. Herpetol. Assoc. Afr. 24:6.
1981 [Pachydactylus weberi] werneri Branch, Ann. Cape Prov. Mus. (Nat. Hist.) 13:145.
1982 Pachydactylus weberi werneri Welch, Herpetology of Africa: 36.
1988 Pachydactylus weberi [part] Branch, Field Guide:208.
1991 [Pachydactylus] weberi werneri Kluge, Smithson. Herpetol. Inform. Serv. 85:24.
1993 [Pachydactylus] weberi werneri Kluge, Gekkonoid Lizard Taxonomy:25.
1994 Pachydactylus weberi [part] Branch, Field Guide, 2nd ed.:208.
1998 Pachydactylus weberi [part] Branch, Field Guide, 3rd ed.:263.
2000 [Pachydactylus] weberi werneri Rösler, Gekkota 2:100.
2001 [Pachydactylus] weberi werneri Kluge, Hamadryad 26:21.
2002 Pachydactylus w[eberi]. werneri Girard, Gekko 3(1):15, 2 figs. P. 16.
2003 Pachydactylus weberi werneri [part] Griffin, Namibian Reptiles:33.
2003 P[achydactylus]. w[eberi]. werneri Bauer \& Lamb, Cimbebasia 19:3.
2005 P[achydactylus]. weberi [part] Bauer and Lamb, Afr. J. Herpetol. 54:116.
Material examined.- Namibia: Maltahöhe District: TM 57276-77, Farm Arbeid Adelt ( $24^{\circ} 06^{\prime}$ S, $16^{\circ} 11^{\prime}$ E); Swakopmund District: TM 34426, 42901. Gobabeb (2315Ca); TM 48179, Hudaob (2315Cb); TM $31346,3 \mathrm{mi}$ N Gorob Mine ( $23^{\circ} 29^{\prime} \mathrm{S}, 15^{\circ} 24^{\prime} \mathrm{E}$ ): TM 57076, E Swakopmund (2214Da); PEM R 16048 (formerly AM 6613 [part]. paralectotype of Pachydactilus werneri), PEM R 16049 (formerly AM 6613 [part], lectotype of $P$. werneri), Khan River (2214Db or 2215A): MB uncatalogued*, MCZ R 183707*, N bank of Swakop River ( $22^{\circ} 38^{\prime} 14^{\prime \prime}$ S. $14^{\circ} 43^{\prime} 39^{\prime \prime}$ E); TM 85001 , Swakop River Bed ( $22^{\circ} 42^{\prime} 26^{\prime \prime}$ S, $14^{\circ} 57^{\prime} 50^{\prime \prime}$ E); TM 50376 , Rössing Mt. (2214Db): NMNW R 5072. Stock Pile Site. Rössing Mine Area ( $22^{\circ} 28^{\prime} \mathrm{S}, 15^{\circ} 02^{\prime} \mathrm{E}$ ); IRSNB 11824 (formerly TM 31761), TM 31757-60, 31762, Palmenhorst on Swakop River (2214Db); NMNW R 4175, $4178,11 \mathrm{~km}$ S of Ostrich Gorge Mouth, Rössing, Khan River ( $22^{\circ} 38^{\prime} \mathrm{S}, 14^{\circ} 56^{\prime} \mathrm{E}$ ); TM 85002 , Swakop River Bed ( $22^{\circ} 42^{\prime} 26^{\prime \prime}$ S, $14^{\circ} 57^{\prime} 50^{\prime \prime}$ E); SMF 45605 , Khan-Mine, 13 mi. E Arandis ( 2215 Ac ); NMNW R 3031, 8978 (2 specimens). TM 32850-52. Khanmine (2215Ac); NMNW R 4262, Panner Gorge nr Khan River ( $22^{\circ} 31^{\prime} \mathrm{S}, 15^{\circ} 01^{\prime} \mathrm{E}$ ); TM 32280-81, Langer Heinrich Game Reserve 3 (2215Cd); Karibib District: NMNW R 4888, NW tributary 1.3 km from Khan River ( $22^{\circ} 20^{\prime} \mathrm{S}, 15^{\circ} 10^{\prime} \mathrm{E}$ ); TM 32853, Vergenoeg 92, Khan River (2215Aa); TM 32302-06, Riet on Swakop River (2215Cb). Additional literature record: Namibia: Swakopmund District: NMWR (as CR 3432), Khan Mine pumping station (2215Ac) (Stuart 1980).

Diagnosis.- To 52.6 mm SVL (TM 31760). Pachydactylus werneri may be distinguished from all other members of the P. serval/weberi group by the combination of the following characters: rostral (and in some cases first supralabial) excluded from nostril; supranasals in variable contact; nostril rims distinctly raised: eyes very large, rostrum pointed; scales on dorsum of head granular. those on snout much larger than those of interorbital region; dorsal scalation heterogeneous,
with relatively small keeled tubercles arranged in 16-18 regular rows; tubercle tips and/or keels often white (Figs. 55-56); thighs with few, small, scattered, keeled to mucronate tubercles; limbs and toes very elongate, slender, toe pads wide; typically 5 undivided lamellae beneath digit IV of pes; tail to approximately $90 \%$ SVL; moderately annulate, bearing whorls of small, keeled, strongly pointed, white-tipped tubercles; adult pattern of diffuse, dark-edged light bands: one on nape, one behind axilla, one on mid-trunk, and one anterior to sacrum; pale bands often not, or barely, lighter than grayish- or pinkish-brown background coloration, pattern often disrupted and appearing as a series of irregular brown cross bands or spots; juvenile pattern similar to adult with four light cross bands (Girard 2002), although often only the nape band is prominent (Fig. 57).

Distribution.- Griffin (2003) considered this species as a Namibian endemic distributed in the Windhoek, Swakopmund, Okahandja, Karibib, Omaruru, Khorixas, Otjiwarango, and Outjo districts. We regard its distribution as being more limited (Karibib, Swakopmund, Maltahöhe districts), corresponding to the lowland areas (chiefly below 1000 m ) north of the southern sand sea of the Namib to just north of the Khan River (Figs. 10-11). Specimens from other portions of Namibia are referable to several new species described herein.

Natural History.- The specimens of Pachydactylus werneri that we collected were active at night on rock faces along the north bank of the Swakop River, and Mertens (1955) found a specimen under a stone. However, according to Mirko Barts (pers. comm., May 2004) the species is not typically rupicolous and is chiefly active on riverine vegetation.

Conservation Status.- Pachydactylus werneri is a Namibian endemic with a rather limited distribution, chiefly along river courses in the Namib. Much of its range occurs within the NamibNaukluft Park and West Coast Recreation Area. Griffin (2003) considered that P. werneri was also expected to occur in several other protected areas, but these areas (e.g., Waterberg Plateau Park, Daan Viljoen Game Park) are occupied by other members of the P. weberi complex. The species is subject to possible habitat degradation from human activities, including mining. It is also susceptible to periodic natural habitat loss associated with the rare flooding events of the Khan, Kuiseb, Swakop and other rivers.

Remarks. - We here designate PEM R 16049 (Fig. 54), an adult female and one of two original syntypes, as the lectotype of Pachydactylus werneri. Given the large number of species now recognized in the serval/weberi complex and the morphological similarity among many of them as well as the previous confusion between this taxon and others in central Namibia, we regard this action as advisable to help stabilize the usage of the name $P$. werneri as here newly re-diagnosed. The juvenile paralectotype, PEM R 16048, is in poor condition.

## Pachydactylus kobosensis FitzSimons, 1938

Figures 58-61.
1938 Pachydactylus kobosensis FitzSimons, Ann. Transvaal Mus. 19:170 (Holotype: TM 17574: Adult male;
"Kobos', 40 miles south of Rehoboth, Great Namaqualand," coll. V. FitzSimons, 21 July 1937. Paratypes:
TM 17517-17519, 17539-40, 17553, 17557-58, MCZ R 46804: same collection data as holotype).
1943 Pachydactylus kobosensis FitzSimons, Mem. Transvaal Mus. 1:74, pl. II, fig. 6, pl. VII, fig. 4, Pl. XIV, fig. 4.
1947 Pachydactylus kobosensis Loveridge, Bull. Mus. Comp. Zool. 98:363.
1955 Pachydactylus kobosensis Mertens, Mertens, Abhandl. Senckenberg. naturf. Ges. 490:46.
1965 Pachydactylus kobosensis Wermuth, Das Tierreich 80:119.
1971 Pachydactylus kobosensis Mertens, Mertens, Abhandl. Senckenberg. naturf. Ges. 529:39.
1982 Pachydactylus kobosensis Welch, Herpetology of Africa:34.
1984 Pachydactylus kobosensis Visser, Lanbouweekbl. 27 April 1984:49, fig. p. 49, middle.
1991 [Pachydactylus] kobosensis Kluge, Smithson. Herpetol. Inform. Serv. 85:23.

1993 [Pachydactylus] kobosensis Kluge, Gekkonoid Lizard Taxonomy:24.
1994 Pachydactylus kobosensis Welch, Lizards of the World 1:93.
2000 [Pachydactylus] kobosensis Rösler, Gekkota 2:98.
2001 [Pachydactylus] kobosensis Kluge, Hamadryad 26:20.
2003 Pachydactylus kobosensis Griffin, Namibian Reptiles:34.
2005 P[achydactylus]. kobosensis Bauer and Lamb, Afr. J. Herpetol. 54:116.
Material examined.- Namibia: Rehoboth District: PEM R 12782-83, MCZ R 46804 (paratype of P. kobosensis, formerly TM 17539), FMNH 64521, TM 17574 (holotype of P. kobosensis), TM 17517-19, $17540,17553,17557-58$ (paratypes of $P$. kobosensis), Kobos, 40 mi . S. Rehoboth ( $23^{\circ} 36^{\prime} \mathrm{S}, 16^{\circ} 44^{\prime} \mathrm{E}$ ); CAS $223903^{*}, 223904^{*}, 223905^{*}, 5.0 \mathrm{~km}$ S Kobos ( $23^{\circ} 37^{\prime} 20^{\prime \prime} \mathrm{S}, 16^{\circ} 41^{\prime} 36^{\prime \prime}$ E); JDV N54680, N54780, vic. Kobos (2316Da); JDV N39880, Rehoboth (2317Ac). Windhoek District: PEM R 12834, Borodino Ranch (2316Cb); JDV 4189-90, 4192, Nauchas ( 2316 Cb ); TM 48441-43, Farm Nauchas 14 ( $23^{\circ} 39^{\prime} \mathrm{S}, 16^{\circ} 18^{\prime} \mathrm{E}$ ).

Diagnosis.- To 53.5 mm SVL (JDV N39880). This is the only member of the $P$. serval/weberi clade in which both the rostral and the first supralabial are typically excluded from the nostril. It may further be diagnosed by the following combination of characters: supranasals in broad contact anteriorly; scales on head flattened or granular, those on snout largest, gradually decreasing in size to small granules on interorbital and parietal regions, no tubercles on head; dorsal scalation largely homogeneous, velvety in appearance, but with scattered enlarged (4-8 times adjacent scales), smooth, flattened to feebly conical scales particularly evident on posterior portion of trunk, especially on sacrum; no tubercles on thighs, or thighs with small, smooth, unkeeled tubercles; digits moderately long, toe pads broadly dilated; typically 6 undivided lamellae under digit IV of pes; adult pattern of more-or-less regular dark bands (entire or broken) extending from flank to flank; tail to at least $113 \%$ SVL, bearing smooth, flattened, well-separated tubercles; both original and regenerated tail frequently thickened basally as a result of fat storage; adult pattern of chocolate brown crossbands and large spots on a pinkish-gray to pinkish-purple background; hatchling and young juvenile color pattern with three dark-bordered bold light bands: on nape, behind axillae and in presacral position (see Visser 1984:49).

Distribution. - This species remains known only from the immediate vicinity of Kobos in the Rehoboth District and from several farms in the southwest Windhoek District (Figs. 10-11). It is likely to be more widespread in granite koppies in central Namibia. All localities are $>1500 \mathrm{~m}$ elevation.

Natural History. - We have collected P. kobosensis from crevices in granite boulders and koppies, similar to those where FitzSimons $(1938,1943)$ found them.

Conservation Status.-Pachydactilus kobosensis is apparently highly restricted in its distribution, but under no obvious threat. Although not yet recorded, it may occur at Oanob Dam and/or in Daan Viljoen Game Park.

Remarks.- This species is among the most distinctive members of the $P$. weberi clade. Although it was never formally synonymized with any other taxon, it was not recognized as valid by Branch (1988) and with the exception of a brief mention by Visser (1984), it appeared only in species lists (e.g.. Kluge 1991, 1993, 2001) until discussed more fully by Griffin (2003). In some specimens from Nauchas, the typical dark dorsal bands of adults are highly fragmented.

## Pachydactylus robertsi FitzSimons, 1938

Figures 62-65.
1938 Pachydactilus robertsi FitzSimons, Ann. Transıaal Mus. 19:177 (Holotype: TM 17854 (Fig. 62): "Farm
‘Kraikluft’. Great Karas Mountains, Great Namaqualand," coll. V. FitzSimons, 12 August 1937).
1943 Pachydactylus robertsi, FitzSimons, Mem. Transvaal Mus. 1:85, pl. XV, fig. 4.

1944 Pachydactylus scutatus robertsi Loveridge, Amer. Mus. Novit. 1254:3.<br>1947 Pachydactylus scutatus robertsi Loveridge, Bull. Mus. Comp. Zool. 98:358.<br>1955 Pachydactylus scutatus robertsi Mertens, Abhandl. Senckenberg. naturf. Ges. 490:48.<br>1965 Pachydactylus scutatus robertsi Wermuth, Das Tierreich 80:122.<br>1971 Pachydactylus scutatus robertsi Mertens, Abhandl. Senckenberg. naturf. Ges. 529:42.<br>1982 Pachydactylus scutatus robertsi Welch, Herpetology of Africa:35.<br>1991 [Pachydactylus] scutatus robertsi Kluge, Smithson. Herpetol. Inform. Serv. 85:23.<br>1993 [Pachydactylus] scutatus robertsi Kluge, Gekkonoid Lizard Taxonomy:25.<br>2000 [Pachydactylus] scutatus robertsi Rösler, Gekkota 2:99.<br>2001 [Pachydactylus] scutatus robertsi Kluge, Hamadryad 26:21.<br>2002 Pachydactylus robertsi Bauer et al., Proc. California Acad. Sci. 53:25, fig. 1.<br>2003 Pachydactylus robertsi Griffin, Namibian Reptiles:34.<br>2005 P[achydactylus]. robertsi Bauer and Lamb, Afr. J. Herpetol. 54:116.

Material examined. - Namibia: Keetmanshoop District: TM 17854 (holotype), Farm Kraikluft, Great Karas Mountains (2718Ba); NMNW R 6696-97*, Farm Kuchanas (2718Ba); CM 119308, 79.5 km S Keetmanshoop (2718Ba).

DIAGNOSIS.- To 42.0 mm (TM 17854). Pachydactylus robertsi may be distinguished from all other members of the $P$. serval/weberi group by the combination of the following characters: rostral excluded from nostril; supranasals in broad contact; scales on snout flattened to weakly conical, much larger than those of interorbital and parietal regions, which consist of relatively small tubercles interspersed among granular scales; dorsal scalation heterogeneous, with approximately 22 rows of large, rounded, flattened, weakly imbricate tubercles bearing very prominent central keels; thighs bearing enlarged keeled or conical tubercles; toes relatively short, toe pads narrow; typically 5 undivided lamellae beneath digit IV of pes; tail to at least $114 \%$ of SVL, moderately annulate, bearing whorls of keeled tubercles, well-separated from one another; adult pattern with a dark-edged white nape band approximately $2-3$ scale rows in width; remainder of dorsum uniform buff to pale brown with small dark flecks relatively uniformly distributed; supralabials white, bordered above by a thick dark brown line passing through orbit (Figs. 62-65); juvenile pattern unknown, probably similar to adult. Pachydactylus robertsi may be distinguished from the unrelated $P$. scutatus, with which it has been confused, on the basis of the exclusion of the rostral from the nostril and its wider nuchal band (typically $2-3$ scale rows vs 1 scale row) (Bauer et al. 2002).

Distribution. - Apparently restricted to the Great Karas Mountains in southern Namibia (Karasburg District) (Figs. 21-22, 30).

Natural History.- FitzSimons (1938) reported the holotype was taken from a rock crack.
Conservation Status.- Pachydactylus robertsi is known from only a single quarter degree square in the Karasberg Mountains. Although no immediate threats to the species are evident, its restricted range make it vulnerable to habitat degradation.

Remarks. - The taxonomic history of $P$. robertsi has been discussed by Bauer et al. (2002) who resurrected the species from the synonymy of $P$. scutatus and considered it as a member of the $P$. weberi complex. The affinities of $P$. robertsi lie with an undescribed species currently known only from Augrabies in the Northern Cape and a single Namibian locality along the lower Orange (see Phylogenetic Relationships).

## Pachydactylus acuminatus FitzSimons, 1941

Figures 66-70.

[^8]1941 Pachydactylus weberi acuminatus FitzSimons, Ann. Transvaal Mus. 20:274 (Syntypes: TM 17689-91, 17693-17695 (Fig. 67): "Aus," coll. V. FitzSimons, 31 July 1937. TM 17722 (Fig. 66): "Konkiep," coll. V. FitzSimons, August 1937. MCZ R 46817 (formerly TM 17692): " 8 miles west of Aus, Great Namaqualand, South West Africa," coll. V. FitzSimons, 31 July 1937).
1943 Pachydactylus montanus onscepensis [part] FitzSimons, Mem. Transvaal Mus. 1:84.
1943 Pachydactylus acuminatus FitzSimons, Mem. Transvaal Mus. 1:90.
1947 Pachydactylus weberi acuminatus Loveridge, Bull. Mus. Comp. Zool. 98:393.
1955 Pachydactylus weberi acuminatus [part] Mertens, Abhandl. Senckenberg. naturf. Ges. 490:49.
1965 Pachydactylus weberi acuminatus [part] Wermuth, Das Tierreich 80:123.
1971 Pachydactylus weberi acuminatus [part] Mertens, Abhandl. Senckenberg. naturf. Ges. 529:43.
? 1981 Pachydactylus w[eberi]. acuminatus [part] Branch, Ann. Cape Prov. Mus. (Nat. Hist.) 13:145.
1982 Pachydactylus weberi acuminatus Welch, Herpetology of Africa:36.
1984 Pachydactylus weberi [part] Visser, Landbouweekbl. 27 April 1984:53, fig. p. 48, bottom, fig. p. 49, top.
1988 Pachydactylus weberi [part] Branch, Field Guide:208.
1991 [Pachydactylus] weberi acuminatus Kluge, Smithson. Herpetol. Inform. Serv. 85:24.
1993 [Pachydactylus] weberi acuminatus Kluge, Gekkonoid Lizard Taxonomy:25.
1994 Pachydactylus weberi [part] Branch, Field Guide, $2^{\text {nd }}$ ed.: 208.
1998 Pachydactylus weberi [part] Branch, Field Guide, 3rd ed.:263.
2000 [Pachydactylus] weberi acuminatus Rösler, Gekkota 2:100.
2001 [Pachydactylus] weberi acuminatus Kluge, Hamadryad 26:21.
2003 Pachydactylus weberi acuminatus Griffin, Namibian Reptiles:33.
2005 P[achydactylus]. weberi [part] Bauer and Lamb, Afr. J. Herpetol. 54:116.
Material examined.- Nambia: Lüderitz District: MCZ R 46877 (syntype, formerly TM 17692), TM 17689-91, 17693-95 (syntypes), 8 mi. W Aus ( $26^{\circ} 38^{\prime} \mathrm{S}, 16^{\circ} 08^{\prime} \mathrm{E}$ ); JDV 30580, 5 km N Aus ( 2616 Cb ); SAM 46652, TM 37120-22, Aus (2616Cb): NMNW R 5408, Aus ( $26^{\circ} 37^{\prime}$ S, $16^{\circ} 20^{\prime}$ E); JDV 1930-32, 2038, 158 km E Lüderitz (2616Da); JDV 2191, 158 km E Kolmanskop (2616Da); Bethanie District: JDV 26080, 26680, 20 km S Helmeringhausen (2516Dd); JDV 30980, Farm Houmoed (2616Ba); JDV 26380, 33280, 35180, 35280, 35380, 36480, 39380, 20 km SW Helmeringhausen (2616Bb); JDV 30680, 30780, 20 km N Bethanien ( 2617 Aa ); TM 17722 (syntype). 20 mi E Konkiep (Goageb Station) ( $26^{\circ} 47^{\prime} \mathrm{S}, 17^{\circ} 32^{\prime} \mathrm{E}$ ); TM 28422, Farm Tiras (2616Ba): JDV 3011. Namibia; Keetmanshoop District: ZMH 01873, railroad track near Keetmanshoop (2618Ca); Maltahöhe District: SAM 45524, 45528, Tsaris Pass (2416Cd); JDV 3351, Farm Duwisib (2516BC): SAM 44623, Sesriem (2415Bd): Swakopmund District: TM 32136, Amichab Mts. Game Res. No. 3 (2315Ba) [locality questionable]. Unknown Locality: JDV 2039, JDV 1065.

Diagnosis. - A large species, to 50.2 mm SVL (TM 30580). Pachydactylus acuminatus may be distinguished from all other members of the $P$. serval/weberi group by the combination of the following characters: nostril rim not strongly inflated, rostral excluded from nostril; supranasals in contact anteriorly; scales on snout and canthus flattened to weakly domed, much larger than those of interorbital and parietal regions, which include tiny granules intermixed with small, weakly-conical tubercles; dorsal scalation highly heterogeneous, with small, oval, weakly to moderately keeled tubercles in 14-18 regular to irregular rows, smallest middorsally and on anterior third of body (approximately $3-5$ times size of adjacent granules): thighs and shanks bearing enlarged conical to mucronate tubercles: toes relatively short. toe pads relatively wide (1.5-2.0 times width of proximal part of digit): typically 6 undivided lamellae beneath digit IV of pes; tail to at least $97 \%$ SVL, annulate, may be expanded greatly basally in association with fat storage, bearing whorls of small, rounded. very weakly-keeled. well-separated tubercles; adult pattern of yellowish- to pinkishbrown with traces of three wide transverse bands (on nape, trunk anterior to midbody, and sacrum) augmented by irregular brown blotches and spots, some with light centers, between bands, sometimes obscuring banding (Figs. 66, 68: see also Visser 1984:48); hatchlings and juveniles with broad, pale (white to grayish), dark-edged bands on the nape, just anterior to midbody, and over
lumbar region (Figs. 69-70; see also Visser 1984:49), occasionaly with one or more additional pale bands on trunk (Fig. 69, right).

Distribution.- This species appears limited to a roughly triangular area between Duwisib, Aus and Keetmanshoop (Figs. 10-11). However, the two easternmost localities, near Keetmanshoop and at Goageb Station, are associated with the same railroad line and it is possible that these animals may have been transported from the Aus region with ore or freight. A locality from the Amichab Mountains is far to the north of authenticated records and is here regarded as questionable and is not plotted on Fig. 11.

Natural History.- FitzSimons (1943) reported that egg size was $10.0 \times 6.5 \mathrm{~mm}$ and that communal egg laying sites, with remains of $50-60$ shells, were used by the species.

Conservation Status.- Nothing is known of the status of this species, but it seems unlikely that it is threatened within the sparsely populated area where it occurs. Griffin (2003) considered it confirmed or likely for the Namib-Naukluft Park, Naute Recreation Resort, and Ai-Ais/Hunsberg Reserve, as well as for the Sperrgebiet. However, we believe that the species as here interpreted may extend only into the Sperrgebiet.

Remarks.- Barbour and Loveridge (1946) referred to MCZ R 46817 as a paratype, but this is incorrect as no holotype was designated in the description of the species. However, TM 17722 (Fig. 66) is the only adult specimen in the type series and the bulk of the species description is based on this specimen.

## Pachydactylus tsodiloensis Haacke, 1966

Figure 71.
1966 Pachydactylus tsodiloensis Haacke, Arnoldia (Rhodesia) 2(25):1, fig. 1, pl. 1 (Holotype: TM 30943:
"Tsodilo Hills, N.W. Ngamiland, Bechuanaland [Botswana] (about $18^{\circ} 42^{\prime}$ S., $21^{\circ} 45^{\prime}$ E., altitude about 1,500
metres)," coll. W.D. Haacke, 17-19 April 1965. PARATYPES: TM 30937-42, 30944-59: same collection data as holotype).
1987 Pachydactylus tsodiloensis Auerbach, Amphib. Reptil. Botswana:85, fig. p. 85.
1988 Pachydactylus tsodiloensis Branch, Field Guide, $1^{\text {st }}$ ed.:208.
1991 [Pachydactylus] tsodiloensis Kluge, Smithson. Herpetol. Inform. Serv. 85:24.
1993 [Pachydactylus] tsodiloensis Kluge, Gekkonoid Lizard Taxonomy:25.
1994 Pachydactylus tsodiloensis Welch, Lizards of the World 1:95.
1994 Pachydactylus tsodiloensis Branch, Field Guide, 2 ${ }^{\text {nd }}$ ed.:208.
1998 Pachydactylus tsodiloensis Branch, Field Guide, 3rd ed.:262, pl. 112, upper right.
2000 [Pachydactylus] tsodiloensis Rösler, Gekkota 2:99.
2001 [Pachydactylus] tsodiloensis Kluge, Hamadryad 26:21.
2003 P[achydactylus]. tsodiloensis Bauer \& Lamb, Cimbebasia 19:3.
2005 P[achydactylus]. tsodiloensis Bauer and Lamb, Afr. J. Herpetol. 54:116.
Material examined.- Botswana: Ngamiland: MB uncatalogued*, SAM 43883-86, TM 30943 (holotype), 30937-42, 30944-59 (paratypes), 46168-72, 46176-81, 46285-86, NMZB-UM 16204, Tsodilo Hills $\left(18^{\circ} 42^{\prime} \mathrm{S}, 21^{\circ} 45^{\prime} \mathrm{E}\right)$.

Diagnosis.- To 60.0 mm SVL (TM 46286; Haacke 1966). May be distinguished from all other members of the $P$. serval/weberi group by the combination of the following characters: rostral (and sometimes $1^{\text {st }}$ supralabial) excluded from nostril; supranasals in broad contact anteriorly or separated by one or more granules; scales on dorsum of head granular, those on snout much comparable in size to largest scales of interorbital region; dorsal scalation heterogeneous, consisting of small flattened scales interspersed with much larger tubercles bearing a single central keel, tubercles becoming larger laterally and conical rather than keeled towards flanks; tubercles in 16-18
rows; thighs bearing enlarged keeled or conical tubercles; toes relatively short, toe pads relatively broad; typically 6-7 under digit IV of pes; tail to at least $125 \%$ of SVL, annulate, bearing whorls of relatively small, keeled, well-separated tubercles; adult pattern yellowish, grayish or russet with regular to irregular thick light (white, gray or yellow) bands with somewhat narrower dark brown borders, either extending across width of body or breaking up onto flanks; usually five (occasionally six) bands: one on nape, one across shoulders, two on mid trunk and one anterior to sacrum (Fig. 71; see also Haacke 1966: plate I; Barts and Haacke 1997, fig. 5; Barts et al. 2001, figs. 1, 5-6); juvenile pattern similar to adult (Haacke 1966, plate I; Barts et al. 2001, figs. 3-4). Dorsal bands may become obscured in larger adults, although a vague alternating light and dark pattern remains discernable.

Distribution.- Endemic to the Tsodilo Hills in Ngamiland, northwestern Botswana (Figs. 10-11). Auerbach (1987) suggested that the range of this species might extend beyond the Tsodilo Hills, but there is no evidence to support this. This is the only member of the group to occur outside of Namibia and South Africa.

Natural History.- Restricted to quartzite and sandstone outcrops (Barts et al. 2001, fig. 2) where they typically emerge at night onto rock surfaces, although they may descend to the ground to cross between boulders (Haacke 1966). Diet in the wild has been reported to include ants (Haacke 1966) as well as termites, spiders and other arthropods (Barts and Haacke 1997; Barts et al. 2001). Data on reproduction and diet in captivity have been reported by Barts and Haacke (1997, 2001) and Barts et al. (2001). Pachydactylus turneri co-occurs in the Tsodilo Hills and has been identified as a possible predator on $P$. tsodiloensis.

Conservation Statcs. - The Tsodilo Hills are remote and have been designated a World Heritage Site because of their many rock paintings. Pachydactylus tsodiloensis is probably under no serious threat from human activity.

Remarks.- Haacke (1966) placed the species in the weberi group without detailed explanation. Auerbach (1987) considered the taxonomic status of the species as "uncertain," but it is unambiguously distinct from all other members of the $P$. weberi group. Bauer and Lamb (2003a) presented evidence that $P$. tsodiloensis is closely related to $P$. waterbergensis.

## Pachydactylus waterbergensis Bauer and Lamb, 2003

Figures 72-74.
1955 Pachydactylus weberi acuminatus [part] Mertens, Abhandl. Senckenberg. naturf. Ges. 490:49. fig. 104.
1971 Pachydactylus weberi acuminatus [part] Mertens, Abhandl. Senckenberg. naturf. Ges. 529:43.
2003 Pachydactylus weberi werneri [part] Griffin, Namibian Reptiles:33.
2003 Pachydactylus waterbergensis Bauer and Lamb, Cimbebasia 19: 5, figs. 1-3.
2005 P[achydactrlus]. waterbergensis Bauer and Lamb. Afi. J. Herpetol. 54:116 (Holotype: NMWN R 6698
(Fig. 72): "Onjoka Settlement. Waterberg Plateau Park [Otjiwarongo District, Otjozondjupa Region,
Namibia, $\left.20^{\circ} 25^{\prime} \mathrm{S}, 17^{\circ} 21^{\prime} \mathrm{E}\right]$," coll. K.P. Erb, 10 November 1993. Paratypes: TM 38268 (Fig. 73),
38285-86: "Waterberg. Otjiwarongo dist. [Otjozondjupa Region]. S.W.A. [Namibia, (SE 2017 Ac, Ad, Ca,
Cb); exact locality not specified]," coll. W.D. Haacke, 4 April 1970; TM 38285-86: "Waterberg,
Otjiwarongo dist. [Otjozondjupa Region]. S.W.A. [Namibia. (SE 2017 Ac, Ad, Ca, Cb); exact locality not
specified]." coll. W.D. Haacke. 5 April 1970; SMF 45679: "Plateau des Grossen Waterberges bei der Farm
Okatjikona." Otjiwarongo District. Otjozondjupa Region. Namibia ( $20^{\circ} 24^{\prime} \mathrm{S}, 17^{\circ} 24^{\prime} \mathrm{E}$ ), coll. R. Mertens, 27 October 1952).

Material Examined.- Nambia: Otjiwarongo District: NMWN R 6698 (holotype), Onjoka Settlement. Waterberg Plateau Park ( $20^{\circ} 25^{\prime} \mathrm{S} .17^{\circ} 21^{\prime} \mathrm{E}$ ): TM 38265-67, 38268 (paratype), 38285-86 (paratypes). Waterberg. exact locality not specified (2017 Ac, 2017Ad, 2017Ca, or 2017Cb); SMF 45679
(paratype), "Plateau des Grossen Waterberges bei der Farm Okatjikona" ( $20^{\circ} 24^{\prime} \mathrm{S}, 17^{\circ} 24^{\prime} \mathrm{E}$ ); TM 84477, Great Waterberg plateau, Farm Waterberg ( $20^{\circ} 20^{\prime} 24^{\prime \prime} \mathrm{S}, 17^{\circ} 14^{\prime} 52^{\prime \prime} \mathrm{E}$ ).

Photographic voucher: Namibia, Otjiwarongo District.- Unnumbered specimen (Fig. 74), Waterberg Plateau, Otjiwarongo District, Otjozondjupa Region, Namibia ( $20^{\circ} 30^{\prime} 24^{\prime \prime} \mathrm{S}$, $17^{\circ} 14^{\prime} 52^{\prime \prime} \mathrm{E}$ ) (Bauer and Lamb 2003a). The tissue sample used in this study was derived from the specimen represented by the photographic voucher.

Diagnosis.- To 49.3 mm (TM 38286). Pachydactylus waterbergensis may be distinguished from all other members of the P. serval/weberi group by the combination of the following characters: rostral excluded from nostril; supranasals very large and in broad contact; scales on dorsum of head flattened to weakly conical, those on snout larger than those of interorbital region; parietal table covered by small, conical tubercles intermixed with even smaller granules; dorsal scalation heterogeneous, smaller conical scales with larger, keeled tubercles in approximately 20 rows; thighs bearing enlarged conical tubercles; toes relatively short, toe pads moderately wide; typically 5 undivided lamellae under digit IV of pes; tail to at least $116 \%$ of SVL, annulate, bearing whorls of small, keeled tubercles, well-separated from one another; adult pattern of narrow, dark-bordered pale (white to yellow) bands on a reddish-brown background: one on nape, one at forelimb insertion, 2-3 on trunk, and one anterior to sacrum; tail with numerous narrow pale bands; juvenile pattern unknown, probably similar to adult.

Distribution.- This species is known only from the Waterberg Plateau Park and the adjacent farms Onjoka and Okatjikona in north-central Namibia (Figs. 10-11).

Natural History.- Found in association with sandstone cliffs, boulders, or exposures.
Conservation Status.- The bulk of the range of this species lies within the Waterberg Plateau Park and thus receives formal protection. The species is secure, but like any highly geographically restricted species, $P$. waterbergensis is potentially vulnerable to habitat destruction.

Remarks.- Bauer and Lamb (2003a) identified this species as the sister species of $P$. tsodiloensis.

## Pachydactylus reconditus Bauer, Lamb, and Branch, sp. nov.

Figures 75-81.

> 1911 Pachydactylus capensis [part] Sternfeld, Fauna dtsch. Kolon. 4(2):14.
> 1911 Pachydactylus Weberi [part] Sternfeld, Fauna dtsch. Kolon. 4(2):14.
> 1911 Pachydactylus Weberi Sternfeld, Mitt. Zool. Mus. Berlin 5:397.
> 1929 Pachydactylus weberi Lawrence, J. S. W. Afr. Sci. Soc. 2:25.
> 1936 Pachydactylus weberi [part] Parker, Novit. Zool. 40:130.
> 1938 Pachydactylus weberi weberi? FitzSimons, Ann. Transvaal Mus. 19:181.
> 1947 Pachydactylus weberi werneri [part] Loveridge, Mem. Mus. Comp. Zool. $98: 394$.
> 1955 Pachydactylus weberi acuminatus [part] Mertens, Abhandl. Senckenberg. naturf. Ges. 490:49.
> 1965 Pachydactylus weberi acuminatus [part] Wermuth, Das Tierreich 80:123.
> 1971 Pachydactylus weberi acuminatus [part] Mertens, Abhandl. Senckenberg. naturf. Ges. 529:43.
> 1984 Pachydactylus weberi [part] Visser, Landbouweekbl. 27 April 1984:53.
> 1993 Pachydactylus weberi [part] Branch, Southern African Snakes:121.
> 1988 Pachydactylus weberi [part] Branch, Field Guide:208, pl. 86, bottom.
> 1994 Pachydactylus weberi [part] Branch, Field Guide, 2nd ed.:208, pl. 86, bottom.
> 1998 Pachydactylus weberi [part] Branch, Field Guide, 3rd ed.:263, pl. 86, bottom.
> 2002 Pachydactylus cf. weberi Bauer et al., Proc. California Acad. Sci. 53:25.
> 2003 Pachydatylus w[eberi]. acuminatus Bauer and Lamb, Cimbebasia 19:3.
> 2003 Pachydactylus weberi werneri [part] Griffin, Namibian Reptiles:33.
> 2005 P[achydactylus]. weberi [part] Bauer and Lamb, Afr. J. Herpetol. 54:116.

Type Material.- Holotype: TM 32838 (Fig. 75): Adult female; Namibia, Khomas Region Windhoek District, Windhoek ( 2217 Ca ), coll. W.J. Steyn and A. Mitchell, 27 February 1965. Paratypes: CAS 231886* (Figs. 76-77): Adult female; Namibia, Hardap Region, Rehoboth District, Oanab Dam, 7 km NW Rehoboth (2316Bb), coll. A.M. Bauer, 19 July 1998. TM 41993 (Fig. 76): Adult male, TM 41994 (Fig. 76): Juvenile female; Namibia, Erongo Region, Karibib District, Farm Komuanab 111 (2215Db), coll. W.D. Haacke, 14 March 1972. NMNW R 3745: Juvenile; Namibia, Khomas Region, Windhoek District, Avis Dam ( $22^{\circ} 33^{\prime} \mathrm{S}$, $17^{\circ} 07^{\prime} \mathrm{E}$ ), coll. H. Berger-Dell'mour, 8 February 1984. NMNW R 3462: Adult male; Namibia, Khomas Region, Windhoek District, Windhoek West, Hippocrates St. ( $22^{\circ} 33^{\prime}$ S, $17^{\circ} 04^{\prime}$ E), coll. H. BergerDell'mour, 1 July 1983. NMNW R 3465: Juvenile; Namibia, Khomas Region, Windhoek District, Windhoek West, Hippocrates St. ( $22^{\circ} 33^{\prime} \mathrm{S}, 17^{\circ} 04^{\prime} \mathrm{E}$ ), coll. H. Berger-Dell'mour, 14 August 1983. NMNW R 10493*: Adult female; Namibia, Khomas Region, Windhoek District, Klein Windhoek (2217Ca), coll. M. Griffin, 18 February 2002.

Additional Material.- Namibia: Rehoboth District: JDV 3009, 80 km N Kalkrand, 26 km W Tsumis (2317Ca); SAM 46645, Gamgam, Tsumis (2317Ca); Windhoek District: TM 31638, Farm Rostock (2315Bd); SMF 45861, Djab (2316Ab); TM 25103, Farm Valencia (2316Ab); TM 57872, Farm Uruganus ( $22^{\circ} 51^{\prime} \mathrm{S}, 16^{\circ} 17^{\prime} \mathrm{E}$ ); ZFMK 33102, Farm Frauenstein (2217Ad); NMNW R 7867, 7869, Otjompaue (2216Db); TM 41526, 12 km S Windhoek (2217Ca); CM 115642, PEM R 12845-46, NMNW R 133, TM 32829, 32832-37, 32839-42, ZFMK 18339, 21949, ZMB 22733, Windhoek (2217Ca); TM 28781-82, NMNW R 10495, number pending, Klein Windhoek ( 2217 Ca ); NMNW R 5387, Moltkeblick, Auas Mts. ( $22^{\circ} 39^{\prime}$ S, $17^{\circ} 10^{\prime}$ E); NMNW R 4684, Krupp St., Suiderhof, Windhoek, Krupp St. ( $22^{\circ} 34^{\prime}$ S, $17^{\circ} 06^{\prime}$ S); NMNW R 3744, Avis Dam, Windhoek ( $22^{\circ} 33^{\prime}$ S, $17^{\circ} 07^{\prime}$ E); NMNW R 3463-64, 3466, 3853-54, Hippocrates St., Windhoek West, ( $22^{\circ} 33^{\prime} \mathrm{S}, 17^{\circ} 04^{\prime} \mathrm{E}$ ): NMNW R 1444, 1533, Goreangab Dam, Windhoek (2217Ca); TM 32826-28, Lichtenstein (2217Cc); TM 31138, Farm Oamites, 20 mi S Windhoek (2217Cc); Karibib District: TM 33650, Horebis Nord (2215Bc); TM 41992, 41995, Farm Komuanab 111 (2215Db); TM 29703, Usakos (2115Dc); JDV 3013, jct. Otjimbingwe and Swakopmund-Windhoek roads (2116Cd); Gobabis District: ZMB 18248, Gobabis (? 2218Bd); Okahandja District: SMF 45678, 65940-43, Okahandja (2116Dd); Omaruru District: SAM 47075, Ugab River at Rd. 76 ( $20^{\circ} 52^{\prime}$ S, $14^{\circ} 57^{\prime}$ E); Imprecise Locality: ZMB 29127, "SüdwestAfrika."

Etymology.- The specific epithet is the Latin word reconditus, meaning hidden or concealed. It refers to the fact that this species, which has long been known from specimens, and which is common in and around Windhoek, has escaped recognition as a distinct species for almost 100 years. The name is formed in the masculine.

Diagnosis.- A mid-sized species, to 44.7 mm SVL (TM 41993). Pachydactylus reconditus may be distinguished from all other members of the $P$. serval/weberi group by the combination of the following characters: nasal region moderately inflated laterally; rostral excluded from nostril; supranasals in broad or narrow contact, or completely separated by internasal granule; scales on snout granular, rounded to oval, domed to very weakly conical; interorbital scales smaller than those of snout, heterogeneous; posterior parts of head covered with small granules intermixed with many larger, rounded, conical tubercles regularly distributed across parietal and temporal regions, changing to dorsal trunk scalation on occiput; dorsal scalation heterogeneous, with large, strongly keeled rounded to oval tubercles arranged in 18-20 rows, largest on midflanks; thighs bearing enlarged conical tubercles; toes relatively short, toe pads relatively narrow; typically 5 undivided lamellae beneath digit IV of pes; tail to $115 \%$ of SVL, annulate, bearing whorls of moderately large, flattened, pointed. weakly-keeled tubercles, becoming conical distally; caudal tubercles usually separated from each other by a single scale; adult pattern pinkish-, yellowish- or reddish-brown or light brown with a dark-edged pale (white, pale yellow or grayish) nape band that may be entire or partially disrupted: remainder of dorsum patterned with regularly distributed, small dark brown markings; tail not banded, bearing scattered dark marks (Figs. 75-78; see also Girard 2002); hatchling pattern uniform light to mid-brown with a discrete pale nape band (e.g., NMNW number pending: Fig. 79): juvenile pattern similar to hatchling (Fig. 80-81) or with three vague pale trunk bands
(two on mid-trunk one presacral) (e.g.,TM 41994; Fig. 76). This species is most similar to $P$. robertsi, from which it may be distinguished by its slightly smaller, non-imbricating dorsal tubercles and wider toe pads.

Description (based on holotype).- Adult female. Snout-vent length (SVL) 42.2 mm . Body relatively depressed, relatively long (TrunkL/SVL ratio 0.44). Head elongate, large (HeadL/SVL ratio 0.29), narrow (HeadW/HeadL ratio 0.64), moderately depressed (HeadH/HeadL ratio 0.36), distinct from neck. Lores and interorbital region weakly inflated. Snout short (Sn-Eye/HeadL ratio 0.34 ), much longer than eye diameter (OrbD/Sn-Eye ratio 0.70 ); scales on snout and forehead smooth, domed to weakly conical; large on snout and canthus becoming smaller and heterogeneous; scales on snout much larger than tiny granules of parietal table. Enlarged, rounded, conical tubercles densely and regularly scattered across interorbital, parietal, and temporal regions as far posterior as occipuit. Eye moderately small (OrbD/HeadL ratio 0.24); orbits without extra-brillar fringes; 5 supracilliary scales at posterodorsal corner of orbit bearing small spines; pupil vertical, with crenelated margins. Ear opening reunded, small (EarL/HeadL ratio 0.07); eye to ear distance slightly greater than diameter of eyes (EyeEar/OrbD ratio 1.05). Rostral approximately $37 \%$ as deep ( 0.4 mm ) as wide (1.1), no rostral groove, contacted by two enlarged supranasals and first supralabials; nostrils oval, oriented laterally, each surrounded by two postnasals, supranasal, and first supralabial; supranasals in contact anteriorly, separated by a single granule posteriorly; dorsal postnasals larger than ventral postnasals, separated by 2-3 granules; nostril rims weakly inflated, bordered posteriorly by a slight depression; one row of scales separate orbit from supralabials; mental wedgeshaped, tapering posteriorly, approximately 2.3 times deeper ( 1.5 mm ) than wide ( 0.7 mm ); no enlarged postmentals or chin shields. Supralabials to angle of jaws 10/8 ( $8 / 7$ to mid-orbit); infralabials $8 / 8$; interorbital scale rows at midpoint of orbit 21 ( 9 across narrowest point of frontal bone).

Dorsal tubercles large ( $10-12$ times size of adjacent scales), largest on midflanks and smallest along dorsal midline, oval, with a pronounced median keel, forming 20 longitudinal rows on trunk; each tubercle surrounded by rosette of small granular scales; ventral scales flattened, imbricate, becoming larger posteriorly, approximately 37 between lowest tubercular rows at midbody; tubercular scales on dorsum at midbody larger than ventral scales at same level; chin granules approximately one sixth to one fourth size of ventral scales, increasing in size gradually on throat. No preanal or femoral pores. Scales on palm, sole, and ventral surface of forelimb smooth, granular; scales on ventral aspect of hindlimbs enlarged, continuous with enlarged scales of precloacal region; scales on dorsal aspect of forelimb smooth proximally, with small conical tubercles intermixed distally; scales on dorsum of thigh and crus greatly enlarged, conical or keeled.

Forelimbs moderately short, stout (ForeaL/SVL ratio 0.13); hindlimbs short (CrusL/SVL ratio 0.15 ); digits relatively short, claws absent; subdigital scansors, except for distalmost, entire, present only on distal portion of toes, 1.2-1.5 times wider than more basal (non-scansorial) subdigital scales; interdigital webbing absent. Relative length of digits (manus): III $>$ IV $>$ II $>\mathrm{V}>\mathrm{I}$; (pes): IV $>$ III $\sim$ V $>$ II $>$ I. Subdigital scansors (excluding small distal divided scansor) I (4), II (4), III (4), IV (4), V (4) - manus; I (4), II (5), III (5), IV (5), V (5) - pes.

Tail sub-cylindrical, depressed; partially regenerated tail longer than snout-vent length (TailL/SVL ratio 1.17; based on CAS 231886); tail relatively thin basally, tapering, with distinct whorls of scales; each transverse row of enlarged, oval, pointed, weakly keeled tubercles separated by $2-3$ rows of smaller scales; adjacent keeled dorsal caudal tubercles generally separated by a single smaller scale; subcaudal scales imbricating; midventral caudal scales enlarged relative to adjacent scales (5-7 times size of dorsal caudal scales); one slightly enlarged, conical, posterodorsallyprojecting postcloacal spur on each side of tailbase.

Coloration (in life): Dorsum pinkish-, yellowish- or reddish-brown to light brown with a dis-
tinct whitish, pale yellow or grayish band bordered anteriorly and posteriorly by narrow dark brown bands, the anterior of which extendining from posteroventral margins of orbit across nape. Remainder of dorsum bearing small, regular, mid- to dark brown spots or blotches, more pronounced anteriorly. A midbrown streak from postnasals to orbit, bordered above by a cream streak from nostril to anterodorsal margin of orbit. Infralabial and posterior supralabial scales white. Scales around orbit yellow. Limbs unpatterned or with faint darker or lighter markings. Tail same color as dorsum, uniform or with small, indistinct somewhat darker markings, caudal tubercles pale yellow. Venter white with very light scattered pigment, especially under limbs and post-pygal portion of tail.

Variation.- Variation in mensural characters of the holotype and most paratypes are presented in Table 2. Neck band broken in some specimens (e.g., paratype TM 41993; Fig. 76), but still clearly discernable. Limbs spotted in some individuals (e.g., TM 41993; Fig. 76). Hatchling (NMNW R number pending; Fig. 79) with uniform mid-brown dorsum and well defined white nape band. Juvenile (TM 41994; Fig. 76) with three very faint trunk bands (anterior and posterior of midtrunk and presacral) in addition to prominent nape band. A juvenile specimen was illustrated by Seufer (1991:124 bottom), showing a yellowish tint to the nape band and dorsal pattern grading from pinkish anteriorly to grayish-brown posteriorly, with pale yellowish tubercle tips on the tail.

Distribution.- Griffin (2003) considered that the species (as P. weberi werneri) occurred in South Africa as well as Namibia, but our results suggest that it is a Namibian endemic. Griffin (2003) cited its occurrence in the Maltahöhe, Bethanie, Keetmanshoop, Lüderitz, and Karasburg districts. Our confirmed localities are all in central Namibia, chiefly at elevations above 1500 m in the Khomas Hochland and adjacent areas (Figs. 10-11). An old eastern record from Gobabis, (Fig. 11, yellow "?") is probably imprecise and may be from anywhere in the Gobabis district as it existed early in the $20^{\text {th }}$ century.

Natural History.- This species is rupicolous and is also found in edificarian habitats in and around Windhoek.

Conservation Status.- Pachydactylus reconditus is widely distributed in central Namibia and is probably under no specific threats. It occurs in several protected areas such as Daan Viljoen Game Park and the Namib-Naukluft Park. In addition, it adapts well to human-altered habitats and occurs on buildings in and around Windhoek.

Remarks.- The first specimens of this form were noted, as $P$. weberi, from Windhoek and Gobabis by Sternfeld (1911a).

## Pachydactylus monicae Bauer, Lamb, and Branch, sp. nov.

Figures 82-87.
1988 Pachydactylus weberi [part] Branch, Field Guide:208.
1994 Pachydactylus weberi [part] Branch, Field Guide, 2nd ed.:208.
1998 Pachydactylus weberi [part] Branch, Field Guide, $3^{\text {rd }}$ ed.:263.
2003 Pachydactylus cf. weberi [part] Bauer and Branch, Herpetol. Nat. Hist. 8:134.
2005 P[achydactylus]. weberi [part] Bauer and Lamb, Afr. J. Herpetol. 54:116.
Type Material.- Holotype: CAS 200034* (Figs. 82-83): Adult male; South Africa, Northern Cape Province, Richtersveld National Park. Sendelingsdrif ( 2816 Bb ), coll. A.M. Bauer, W.R. Branch and D.A. Good. 20 September 1995. Paratypes: CAS 200079* (Fig. 85): Juvenile mlae; South Africa, Northern Cape Province. Richtersveld National Park. Sendelingsdrif (2816Bb), coll. A.M. Bauer and D.A. Good, 30 September 1995. CAS 193406*: Adult male: South Africa, Northern Cape Province, Richtersveld National Park. Potjiespram. S bank of Orange River (2816Bb), coll. A.M. Bauer, H.E. Robeck, D. King and J.V. Vindum. 30 June 1993. CAS 193417: Juvenile; South Africa, Northern Cape Province, Richtersveld National

Park, Sendelingsdrif (2816Bb), coll. A.M. Bauer, H.E. Robeck, D. King and J.V. Vindum, 30 June 1993. PEM R 7626: Adult female; South Africa, Northern Cape Province, Richtersveld National Park, Reuning Mine (2816Bb), coll. H.H. Braack (no date of collection recorded). PEM R 11952: Adult female; South Africa, Northern Cape Province, Richtersveld National Park, Sendelingsdrif ( $28^{\circ} 07^{\prime} \mathrm{S}^{\circ}, 16^{\circ} 53^{\prime} \mathrm{E}$ ), 50 m , coll. W.R. Branch. A.M. Bauer and D.A. Good, 20 September 1995. TM 33806: Adult female; South Africa, Northern Cape Province, Richtersveld National Park, Swartpoort (2816Bb), coll. W.D. Haacke, 25 September 1967. TM 36367: Adult female; Namibia, Karas Region, Karasburg District, Fish River Canyon (bottom at viewing point) (2717Da), coll. W.D. Haacke, May 1963. TM 41852: Adult male; Namibia, Karas Region, Karasburg District, Farm Holoog ( 2717 Bd ), coll. W.D. Haacke, March 1972. TM 28297: Adult male; Namibia, Karas Region. Karasburg District, Fish River Canyon ( $27^{\circ} 35^{\prime} \mathrm{S}, 17^{\circ} 37^{\prime} \mathrm{E}$ ), coll. W.D. Haacke, December 1962.

Additional Material.- South Africa: Northern Cape Province: PEM R 1959, above Springbokvlakte, Richtersveld National Park (2817Ca); CAS 193418*, 193419, 200049, LSUMZ 57343-44, PEM R 7324-25, 11952, Sendelingsdrif, Richtersveld National Park (2816Bb). Namibia: Lüderitz District: TM 35457, 10 mi . NW Fish River Mouth (2817Aa); CAS 201879*, 7.6 km W of Fish River Mouth ( $28^{\circ} 03^{\prime} 43^{\prime \prime} \mathrm{S}, 17^{\circ} 07^{\prime} 25^{\prime \prime}$ ); NMNW R 178 ( 2 specimens), TM 35362, Farm Namuskluft (2716Dd); [?] PEM R 12866. Obib Mts. (2816Ba); CAS 201887*, NMNW 8869, Witputz Sud, ca. 40 km N Rosh Pinah ( $27^{\circ} 40^{\prime} 18^{\prime \prime} \mathrm{S}$, $16^{\circ} 43^{\prime} 10^{\prime \prime}$ E); TM 35384, Farm Spitzkop (2716Dc); Karasburg District: TM 41854-57, Farm Holoog (2717Bd): TM 27977, 28298. Fish River Canyon ( $27^{\circ} 35^{\prime}$ S, $17^{\circ} 37^{\prime} \mathrm{E}$ ); SAM 43488, TM 32830-31, 32865, AiAis ( 2717 Cd ); NMNW 8856, Ai-Ais Nature Reserve, c. 3 km N Orange River ( $28^{\circ} 12^{\prime} 26^{\prime \prime} \mathrm{S}, 17^{\circ} 16^{\prime} 43^{\prime \prime} \mathrm{E}$ ); TM $47014,2 \mathrm{~km}$ NE Ai-Ais (2717Dc); JDV N26080, 20 km N Ai-Ais (2717Dc).

Etymology.- The specific epithet is a matronym honoring Monica Frelow Bauer, wife of the senior author, for her tolerance of long absences in the field and long hours in the laboratory and her support of systematic herpetology. The name is constructed in the feminine genitive.

Diagnosis.- A large species, to 47.9 mm SVL (TM 36367). Pachydactylus monicae may be distinguished from all other members of the $P$. serval/weberi group by the combination of the following characters: nostril rim not strongly inflated laterally; rostral excluded from nostril; supranasals in variable contact; scales on snout and canthus smooth, flattened to weakly domed; interorbital and parietal regions with smaller granules interspersed with domed to weakly conical tubercles; scales on snout comparable in size to interorbital tubercles, much larger than granular scales of parietal table; dorsal scalation heterogeneous, with moderately large, rounded, strongly keeled tubercles in 16-18 regular rows; thighs bearing scattered moderately enlarged conical to keeled tubercles: toes relatively short, toe pads relatively wide; typically five undivided lamellae beneath digit IV of pes; tail annulate, bearing whorls of moderately large, oval, strongly keeled tubercles, some with striated surfaces, usually separated from each other by a single narrow scale; adult pattern of three broad pale bands (one on nape, one anterior of midbody, one on lumbar region), each bordered by narrow dark edges, on a grayish- to yellowish-brown background; dark edges often fade with age/size and dark speckles in interspaces between bands, and within pale bands can result in obscuring of bands (Figs. 82-84); tail with alternating yellowish-brown and much narrower mid-brown bands; hatchling with dark brown body with pale transverse bands in same positions as adult, dark brown becoming paler in juveniles, yielding a bold banded pattern of alternating brown to grayish-brown and whitish to pale yellowish bands, separated by narrow dark brown to blackish borders; larger juveniles usually with stray dark markings between bands, as in adults (Figs. 85-87).

Description (based on holotype).- Adult male. Snout-vent length (SVL) 44.1 mm . Body relatively depressed, relatively short (TrunkL/SVL ratio 0.42). Head elongate, large (HeadL/SVL ratio 0.31), narrow (HeadW/HeadL ratio 0.61), moderately depressed (HeadH/HeadL ratio 0.36), distinct from neck. Lores and interorbital region somewhat inflated. Snout short (Sn-Eye/HeadL ratio 0.33), much longer than eye diameter (OrbD/Sn-Eye ratio 0.71); scales on snout and forehead smooth, flattened to domed; large on snout and canthus, becoming granular on interorbital region with larg-
er, weakly conical tubercles, approximately same size as snout scales, interspersed; scales on snout much larger than granular scales of parietal table. Enlarged conical tubercles regularly scattered across interorbital, parietal and temporal regions as far posterior as nape. Eye moderately small (OrbD/HeadL ratio 0.24 ); orbits without extra-brillar fringes; approximately 8 supracilliary scales at posterodorsal corner of orbit bearing small spines; pupil vertical, with crenelated margins. Ear opening oval, more-or-less horizontally oriented, moderate (EarL/HeadL ratio 0.08); eye to ear distance equal to diameter of eyes (EyeEar/OrbD ratio 1.00). Rostral approximately 50\% as deep ( 0.8 mm ) as wide (1.5), no rostral groove, contacted by two enlarged supranasals and first supralabials; nostrils oval, oriented laterally (L) or anteriorly (R), each surrounded by two postnasals, supranasal, and first supralabial; supranasals in contact anteriorly, separated by a single granule posteriorly; dorsal postnasals larger than ventral postnasals, separated by 3 granules; nostril rims very weakly inflated, bordered posteriorly by a slight depression; one row of scales separate orbit from supralabials; mental with nearly parallel sides, tapering only slightly posteriorly, approximately 2.6 times deeper ( 1.8 mm ) than wide $(0.7 \mathrm{~mm})$; no enlarged postmentals or chin shields. Supralabials to angle of jaws $10 / 10$ ( $8 / 8$ to mid-orbit); infralabials $8 / 8$; interorbital scale rows at midpoint of orbit 24 ( 7 across narrowest point of frontal bone).

Dorsal tubercles relatively small (4-6 times size of adjacent scales), largest on midflanks and smallest along dorsal midline, oval, with a pronounced median keel, forming 16 regular longitudinal rows on trunk; each tubercle surrounded by rosette of small granular scales; ventral scales flattened, oval, subimbricate to imbricate, becoming larger posteriorly, largest on posterior abdomen and in precloacal region, approximately 24 between lowest granular rows on flank at midbody; tubercular scales on dorsum at midbody larger than ventral scales at same level; chin granules approximately one third to one fourth size of ventral scales, increasing in size rather abruptly on throat. No preanal or femoral pores. Scales on palm, sole, and ventral surface of forelimb smooth, granular; scales on ventral aspect of thighs enlarged, continuous with enlarged scales of precloacal region; scales on dorsal aspect of forelimb smooth, juxtaposed to subimbricate proximally, with small conical tubercles intermixed distally; scales on dorsum of thigh and crus enlarged, conical.

Forelimbs moderately long, stout (ForeaL/SVL ratio 0.14); hindlimbs moderately long (CrusL/SVL ratio 0.17); digits relatively short, claws absent; subdigital scansors, except for distalmost, entire, present only on distal portion of toes, approximately 1.5 times wider than more basal (non-scansorial) subdigital scales; interdigital webbing absent. Relative length of digits (manus): III $>$ IV $>$ II $>$ V $>$ I; (pes): IV $>$ III $\sim$ V $>$ II $>$ I (most of digits I and II of right manus missing in holotype). Subdigital scansors (excluding small distal divided scansor) I (4), II (4), III (4), IV (4), V (4) - manus; I (4), II (5), III (5), IV (5), V (5) - pes.

Tail sub-cylindrical, somewhat depressed; partially regenerated tail longer than snout-vent length (TailL/SVL ratio 1.02); tail moderately thick basally, tapering, with distinct whorls of scales; each transverse row of enlarged, oval, strongly keeled tubercles separated by 3-4 rows of smaller scales; adjacent keeled dorsal caudal tubercles separated by a single smaller, often narrow and elongate scale; subcaudal scales subimbricating to imbricating, enlarged ( $3-5$ times dorsal caudal scales), midventral scales not much enlarged relative to adjacent subcaudals; two enlarged, pointed, partly recurved postcloacal spurs on each side of tailbase, anterior considerably larger than posterior.

Coloration (in life): Dorsum beige or yellowish- or grayish-brown with three wide, pale transverse bands with narrow mid-brown borders. First band across nape and continuing anteriorly through ventral half of orbit. Second band on trunk anterior to midbody, third extending forward from anterior margin of hindlimb insertion. Scattered light to mid-brown flecks across the entire dorsum, both between and within pale transverse bands. Dorsum of head with small, scattered
brown spots and dashes. A thick midbrown line from nostril through orbit to above ear, continuous with anterior dark border of nape band. A faint brown streak from supranasals posteriorly along dorsal midline to level of anterior orbit. Dorsal circumorbital scales pale yellow, ventral circumorbital scales white. Anterior supralabials brown; posterior supralabials and all infralabials white with scattered brown pigment spots. Limbs same color as dorsum with scattered darker markings. Tail with alternating beige and mid-brown bands; the former 2-3 times width of latter. Caudal tubercles and those of flanks with whitish tips. Venter white to cream with very faint scattered pigment along edges of flanks, chin and limbs.

Variation.- Variation in mensural characters of the holotype and paratypes are presented in Table 3. Paratypes similar to holotypes in most scalation features. Three cloacal spurs on each side of tail base in TM 41852 . Hatchlings (e.g. TM 32830, SVL 19.5 mm ; Fig. 86) with dark brown trunk with dark-edged cream bands across nape, anterior midtrunk and presacral region. Tail with discrete alternating dark brown and cream annuli, cream annuli approximately twice width of brown. Larger juveniles ( $23.2-30.6 \mathrm{~mm}$ SVL; e.g. CAS 193417) with dorsal background coloration faded to light brown, transverse bands bold and strongly contrasting. Larger individuals with varying degrees of scattered brown markings on dorsum, always between pale transverse bands and in larger individuals within these bands as well. Bands faded to near background color, but still discernable, in largest specimens (e.g., TM 33806; Fig. 84). Color blanched in PEM paratypes. Specimens from Farm Holoog especially boldly patterned, with few if any stray markings between or within transverse bands (Figs. 84-85).

Distribution.- Pachydactylus monicae is distributed in and around the lower Orange River Valley and lower Fish River Valley and its tributary, the Holoog River (Figs. 21-22, 30). In the west it reaches the Rosh Pinah area in the Lüderitz District. In the Northern Cape Province of South Africa it has thus far been collected only along the Orange River in the Richtersveld National Park. It is sympatric with another new species in the weberi group throughout much of its range, and with $P$. weberi at Sendelingsdrif in the Richtersveld.

Natural History.- This is one of the most terrestrial species in the P. weberi group. It is almost exclusively restricted to riverine environments (Fig. 88). At Sendelingsdrif it has been collected underneath trash and other debris some distance from rocky areas. The holotype was collected in a pile of logs. One specimen (CAS 200049) was found dessicated in an unused garage at Sendelingsdrif. Elsewhere it occupies boulder outcrops in relatively mesic low elevation areas (Fig. 89).

Conservation Status.- Virtually the entire range of P. monicae occurs within the AiAis/Richtersveld Transfrontier Park, where it is adequately protected. However, its restriction to riverine environments makes it susceptible to habitat damage from periodic floods, alluvial mining activity and other perturbations.

## Pachydactylus griffini Bauer, Lamb, and Branch, sp. nov.

Figures 90-92.

> 1914 P[achydactylus] purcelli [part] Methuen and Hewitt, Ann. Transvaal Mus. 4:131.
> 1947 Pachydactylus purcelli [part] ? Loveridge, Bull. Mus. Comp. Zool. 98:362.
> 2005 P[achydactylus]. serval [part] Bauer and Lamb, Afr. J. Herpetol. 54:116.

Type Material.- Holotype: CAS 125855 (Fig. 90): Subadult female; Namibia, Karas Region, Keetmanshoop District, 4 mi NW Aroab on rd. to Keetmanshoop (2619Dc), coll. T.J. Papenfuss, 13 May 1970. Paratypes: CAS 125854 (Fig. 91): Adult female; same collection data as holotype. CAS 186294* (Fig. 91): Adult male, CAS 186295 (Fig. 92): Juvenile; Namibia, Karas Region, Karasburg District, Farm Narudas, 0.5 km N of house (2718Bd), coll. A.M. Bauer, 10 July 1992. MCZ R 163286 (formerly JDV 31680) (Fig. 91):

Adult male; Namibia, Karas Region, Keetmanshoop District, between Narubis and Aroab (2619C, 2619D, 2719A or 2719B), coll. J.D. Visser, 4 August 1980. TM 3099 (Fig. 92): Juvenile; Namibia, Karas Region, Karasburg District, Narudas Süd ( $27^{\circ} 21^{\prime}$ S, $18^{\circ} 51^{\prime}$ E), coll. P.A. Methuen, 30 October 1912.

Etymology.- The specific epithet of this Namibian endemic is a patronym honoring Mike Griffin, Senior Support Specialist, Ministry of the Environment and Tourism, Windhoek, Namibia. Mr. Griffin has contributed greatly to the knowledge and conservation of the herpetofauna of Namibia and for many years has provided support and advice during our research expeditions to Namibia. The name is constructed in the masculine genitive.

Diagnosis.- A small species, to 39.4 mm SVL. Pachydactylus griffini may be distinguished from all other members of the $P$. serval/weberi group by the combination of the following characters: snout strongly inflated laterally; rostral enters nostril; supranasals in narrow or broad contact; scales on dorsum of head uniform and granular, those on snout larger than those of interorbital region; no tubercles on parietal table; dorsal scalation largely homogeneous, with small, scattered, flattened, weakly keeled tubercles in four rows, two on each dorsolateral margin of abdomen and sacrum; thighs without tubercles; toes relatively long, slender, toe pads relatively wide; five undivided lamellae beneath digit IV of pes; tail to at least $88 \%$ of SVL (no adult specimens with original tail), weakly annulate, bearing whorls of small, weakly keeled, pointed tubercles with striated surfaces, usually separated from each other by single scales; adult pattern of small, mostly rounded, spots evenly distributed across dorsum, with some trace of two transverse, thin, dark lines or rows of spots across occiput and nape (Figs. 90-91); juvenile pattern as adult, this is the only member of the group to have spotted hatchlings and juveniles (Fig. 92).

Description (based on holotype). - Adult female. Snout-vent length (SVL) 30.3 mm . Body relatively depressed, moderately long (TrunkL/SVL ratio 0.45). Head elongate, large (HeadL/SVL ratio 0.29), relatively wide (HeadW/HeadL ratio 0.68), somewhat depressed (HeadH/HeadL ratio 0.36 ), distinct from neck. Lores and interorbital region strongly inflated. Snout short (SnEye/HeadL ratio 0.35), longer than eye diameter (OrbD/Sn-Eye ratio 0.73 ); scales on snout and forehead round to oval, flattened, granular becoming weakly conical near anterior border of orbits; scales on snout slightly larger than those of anterior interorbital area, much larger than those of parietal table. Eye moderately large (OrbD/HeadL ratio 0.26); orbits without extra-brillar fringes; 3-4 supracilliary scales at posterodorsal corner of orbit bearing small spines; pupil vertical,with crenelated margins. Ear opening oval, large (EarL/HeadL ratio 0.10), angled posterodorsally at 45\% to horizontal; eye to ear distance less than diameter of eyes (Eye-Ear/OrbD ratio 0.87) [slightly greater than diameter of eyes in paratypes]. Rostral less than $50 \%$ as deep ( 0.6 mm ) as wide (1.2); no rostral groove; contacted by two enlarged supranasals and first supralabials; nostrils oval, oriented laterally and slightly dorsally, each surrounded by rostral, two postnasals, supranasal, and first supralabial; supranasals in broad contact; dorsal postnasals twice size of ventral postnasals, separated by three granules; nostril rims weakly inflated; one row of scales separate orbit from supralabials; mental wedge-shaped, approximately 1.6 times deeper ( 1.2 mm ) than wide ( 0.7 mm ); no enlarged postmentals or chin shields. Supralabials to angle of jaws 10/10 (8/8 to mid-orbit); infralabials 10/9; interorbital scale rows at midpoint of orbit 22 ( 7 across narrowest point of frontal bone).

Dorsal scales small, granular. Tubercles small ( $2-3$ times size of adjacent scales), rounded, with a weak median keel, in four rows - two on each dorsolateral margin of the trunk, chiefly over sacrum and abdomen: ventral scales flattened, imbricate, becoming somewhat larger posteriorly, approximately 29 between lowest rows of granular scales on flanks at midbody; scales on venter at midbody much larger than those on dorsum at same level; chin granules approximately one third to one fourth size of ventral scales, increasing gradually in size on throat. No preanal or femoral pores. Scales on palm and sole granular to weakly conical; ventral surface of shank and forearm with
smooth, imbricating scales with ctenate free margins; preaxial surfaces of basal limb segments with smooth, enlarged, imbricating scales grading into juxtaposed granules on postaxial surfaces; scales on ventral aspect of thighs enlarged.

Forelimbs moderately short, stout; forearm short (ForeaL/SVL ratio 0.16); hindlimbs relatively short, tibia moderately short (CrusL/SVL ratio 0.17); digits relatively long, claws absent; subdigital scansors, except for distalmost, entire, present only on distal portion of toes, 1.5-2.0 times wider than more basal (non-scansorial) subdigital scales; interdigital webbing absent. Relative length of digits (manus): III $>$ IV $>$ II $\sim$ V $>$ I; (pes): IV $>$ III $\sim$ V $>$ II $>$ I. Subdigital scansors (excluding small distal divided scansor) I (4), II (4), III (4), IV (4), V (4) - manus; I (4), II (5), III (5), IV (5), V (5) - pes.

Tail sub-cylindrical, weakly depressed; partially regenerated tail shorter than snout-vent length (TailL/SVL ratio 0.87); tail relatively thin basally, tapering, with distinct whorls of scales; each transverse row of smooth oval tubercles separated by 3 rows of smaller scales; smaller scales rectangular with rounded free margins; subcaudal scales rounded, pointed posteriorly, larger than dorsal caudal scales; scales of midvental row larger than adjacent rows; a single, slightly enlarged, rounded, dorsally-projecting postcloacal spur on each side of tailbase.

Coloration (in preservative): Dorsal color straw, with small, rounded, evenly distributed light brown spots arranged in 4-6 relatively regular longitudinal rows on trunk. A thin, transverse, light brown line across occiput and another shorter line and three spots forming an incomplete line across nape. Pareital table, interorbital area and snout with scattered brown spots and blotches. A brown line from nostril, through center of eye, over ear to level of transverse occipital line. Anterior supralabial scales midbrown; more posterior supralabials and all infralabials cream to straw with a tinge of brown pigment on labial margins. Limbs with scattered clusters of light brown scales, forming weakly defined spots. Tail with small brown spots, like dorsum, with white tubercles. Venter buff, without pigmentation. Methuen and Hewitt (1914) indicated that the color of the paratype TM 3099 in life was straw with black markings.

Variation.- Comparative mensural data for holotype and adult paratypes presented in Table 4. Paratypes CAS 186294 and MCZ R 163286 (Fig. 91) have larger dorsal spots than the holotype and have the occipital band incomplete. Male paratypes have cloacal spurs consisting of 2-3 enlarged, pointed, anterodorsally projecting scales. Juvenile paratypes CAS 186295 ( 22.1 mm SVL) and TM 3099 ( 27.9 mm SVL) with similar spotted pattern as holotype and adult paratypes (Fig. 92). TM 3099 with somewhat larger, darker spots, tail with incomplete brown crossbands as well as spots. CAS 186295 with both occipital and nape markings broken, limbs not spotted. Original tail in TM 3099 105\% of SVL.

Distribution.- This species has been found at three localities in and around the Karasberg Mountains in southeastern Namibia (Figs. 30-31). All known localities are above 1000 m in elevation. The eastern-most locality, near Aroab, is essentially at the western edge of the Kalahari and is further east than any localities for P. serval sensu lato plotted by either Visser (1984) or Branch (1988, 1998). Pachydactylus griffini is sympatric with P. purcelli at Farm Narudas.

Natural History.- Methuen and Hewitt reported that TM 3099 was collected on sandy soil, as were CAS 186294-95. Although habitat details are lacking for the other members of the type series, they come from localities at the western edge of the Kalahari and may also be associated with sand.

Conservation Status.- Pachydactylus griffini has a highly restricted range, although it is undoubtedly more common than the existing collections suggest. Its known range does not encompass any protected areas within Namibia.

Remarks. - The presence of two forms of the $P$. serval group at Narudas was first signaled
by Methuen and Hewitt (1914), who noted that TM 3099 (Fig. 92) differed in appearance and habitat from the other $P$. purcelli (actually a composite series of P. purcelli and $P$. montanus) they collected in the Karasburg region. Loveridge (1947) also noted that this specimen was problematic and only tentatively allocated it to P. purcelli. In fact, three species of serval-type geckos (purcelli, onscepensis, griffini) as well as one weberi-type species cooccur in sympatry at the Farm Narudas. The one specimen of this species sequenced showed its greatest genetic affinities with Pachydactylus carinatus, but it is most similar morphologically to $P$. serval and $P$. montanus.

## Pachydactylus mclachlani Bauer, Lamb, and Branch, sp. nov.

Figures 93-98.
? 1981 Pachydactylus w[eberi]. acuminatus [part] Branch, Ann. Cape Prov. Mus. (Nat. Hist.) 13:145. 2005 P[achydactylus]. weberi [part] Bauer and Lamb, Afr. J. Herpetol. 54:116.

Type Material. - Holotype: NMNW R 10499 (Fig. 93): Adult male; Namibia, Karas Region, Karasburg District, Noordoewer ( $28^{\circ} 39^{\prime} 48^{\prime \prime} \mathrm{S}, 17^{\circ} 49^{\prime} 23^{\prime \prime} \mathrm{E}$ ), coll. M. Griffin, 11 April 1997. Paratypes: NMNW R 10496: Adult female, NMNW R 10497: Juvenile, NMNW R 10498: Adult male; Namibia, Karas Region, Karasburg District. Haib Mine ( $28^{\circ} 41^{\prime} 49^{\prime \prime} \mathrm{S}, 17^{\circ} 53^{\prime} 26^{\prime \prime} \mathrm{E}$ ), coll. M. Griffin, 10 April 1997. CAS 186293 (Fig. 94): Adult female; Namibia, Karas Region, Karasburg District, Farm Narudas, 0.5 km N of house (2718Bd), coll. A.M. Bauer, 10 July 1992. CAS 125850, 125852: Adult females, CAS 125853: Adult male, CAS 125851: Juvenile; Namibia, Karas Region, Keetmanshoop District, 4 mi. NW Aroab on rd. to Keetmanshoop (2619Cc), coll. T.J. Papenfuss, 13 May 1970. CAS 186287: Juvenile; Namibia, Karas Region, Karasburg District, Farm Narudas at River (2718Bd), coll. A.M. Bauer, 10 July 1992. CM 119309 (Figs. 95, 97): Adult female, CM 119310-11: Juveniles; Namibia, Karas Region, Keetmanshoop District, 79.5 km S Keetmanshoop (2718Ba), coll. P. Freed, 28 March 1990. TM 54735 (Figs. 95-96): Adult female; Namibia, Karas Region, Karasburg District, Farm Sperlingsputs 259 ( $28^{\circ} 43^{\prime}$ S, $18^{\circ} 13^{\prime}$ E), coll. J. Lougher, July 1980.

Etymology.- The specific epithet is a patronym honoring the late Geoff McLachlan (1923-2005), ornithologist and herpetologist, former director of the Port Elizabeth Museum and later Curator of Herpetology at the South African Museum. Geoff devoted much of his later life to the study of Pachydactrlus and his pioneering studies on P. serval and its relatives highlighted the taxonomic difficulties of this group. The name is constructed in the masculine genitive.

Diagnosis.- A moderately large species, to 48.7 mm SVL (NMNW R 10496). Pachydactylus mclachlani may be distinguished from all other members of the $P$. serval/ weberi group by the combination of the following characters: nasal region moderately inflated; rostral narrowly excluded from nostril; supranasals in broad or narrow contact anteriorly; scales on snout and canthus granular, rounded to oval, flattened to weakly domed, much larger than granular scales of interorbital and parietal regions; small, rounded. conical tubercles, smaller than snout scales, interspersed among granules of interorbital and parietal regions: dorsal scalation heterogeneous, with moderately large, oval, strongly keeled tubercles arranged in 14-18 regular rows; thighs bearing enlarged conical tubercles; toes relatively long, toe pads moderately broad: typically six undivided lamellae beneath digit IV of pes: tail to at least $112 \%$ of SVL. annulate, bearing whorls of slightly enlarged, oval, flattened to weakly keeled tubercles, each well-separated from one another; adult pattern midbrown to purplish-brown with two thin light (cream to grayish- or purplish-brown) transverse bands, one on nape and one on trunk anterior to midbody. A broader pale band, just anterior to the hindlimb insertion, is less well developed or inconspicuous in some adults (Figs. 93-97). In some larger specimens the basic pattern is augmented by additional dark spots and incomplete bars; tail uniform brown to grayish-brown or with weakly contrasting alternating light and dark segments, caudal tubercles whitish: juvenile pattern very dark brown trunk with lighter head, a pale nape band and very thin anterior trunk band. area from just anterior to sacrum to tail base, including hindlimbs, ashy to pale purplish-brown. with or without a dark band across pygal portion of tail; tail orange.

Description (based on holotype). - Adult male. Snout-vent length (SVL) 43.0 mm . Body relatively depressed, moderately long (TrunkL/SVL ratio 0.39). Head relatively short (HeadL/SVL ratio 0.30 ). moderately wide (HeadW/HeadL ratio 0.67), somewhat depressed (HeadH/HeadL ratio 0.36 ). distinct from neck. Lores and interorbital region inflated. Snout moderately long (SnEye/HeadL ratio 0.36), longer than eye diameter (OrbD/Sn-Eye ratio 0.72); scales on snout and canthus large, smooth, flattened to domed; scales of interorbital and parietal regions strongly heterogeneous, with tiny granules interspersed with larger, domed to conical, rounded tubercles, each $50-70 \%$ size of large snout scales. Enlarged conical tubercles regularly scattered across occipital and temporal regions as far posterior as nape. Eye moderate (OrbD/HeadL ratio 0.26); orbits without extra-brillar fringes; 4-5 supracilliary scales at posterodorsal corner of orbit bearing very small spines; pupil vertical, with crenelated margins. Ear opening oval, angled at $45 \%$ to horizonatal, large (EarL/HeadL ratio 0.11); eye to ear distance equal to diameter of eyes (EyeEar/OrbD ratio 1.01). Rostral approximately $55 \%$ as deep ( 0.8 mm ) as wide (1.4), no rostral groove, contacted by two enlarged supranasals and first supralabials; nostrils oval, oriented laterally, each surrounded by two postnasals, supranasal, and first supralabial; supranasals in contact anteriorly, separated by a single granule posteriorly; dorsal postnasals much larger than ventral postnasals, separated by a single granule; nostril rims weakly inflated, bordered posteriorly by a distinct notch; 1-2 rows of scales separate orbit from supralabials; mental with nearly parallel sides, approximately 2.4 times deeper ( 1.9 mm ) than wide $(0.8 \mathrm{~mm})$; no enlarged postmentals or chin shields. Enlarged supralabials to angle of jaws 13/13 ( $9 / 9$ to mid-orbit); infralabials $8 / 8$; interorbital scale rows at midpoint of orbit 22 ( 9 across narrowest point of frontal bone).

Dorsal tubercles large ( $8-10$ times size of adjacent scales), largest on midflanks and smallest along dorsal midline and on anterior one third of trunk, rounded, with a pronounced median keel, forming 14 regular longitudinal rows on trunk, grading into conical granular scales on lower flanks; each tubercle surrounded by a regular to irregular rosette of small granular scales; ventral scales flattened, oval, subimbricate to imbricate, becoming larger posteriorly, largest on posterior abdomen and in precloacal region, approximately 35 between lowest conical granular rows on flank at midbody; tubercular scales on dorsum at midbody much larger than ventral scales at same level; chin granules approximately one fourth size of ventral scales, increasing in size rather abruptly on throat. No preanal or femoral pores. Scales on palm, sole, and ventral surface of forelimb smooth, granular; scales on ventral aspect of thighs enlarged, continuous with enlarged scales of precloacal region; scales on dorsal aspect of forelimb smooth, heterogeneous, subimbricate; scales on dorsum of thigh and crus greatly enlarged, conical.

Forelimbs short, stout (ForeaL/SVL ratio 0.16); hindlimbs short (CrusL/SVL ratio 0.17); digits relatively long, claws absent except for minute stylets on digits II and V of pes; subdigital scansors, except for distalmost, entire, present only on distal portion of toes, approximately 1.3 times wider than more basal (non-scansorial) subdigital scales; interdigital webbing absent. Relative length of digits (manus): III $>$ IV $>$ II $>$ V $>$ I; (pes): IV $>$ III $\sim$ V $>$ II $>$ I (distal portion of digit IV of left pes missing in holotype). Subdigital scansors (excluding small distal divided scansor) I (4), II (4), III (4), IV (4), V (4) - manus; I (5), II (5), III (5), IV (6), V (6) - pes.

Tail sub-cylindrical, weakly depressed; original tail longer than snout-vent length (TailL/SVL ratio 1.09; based on CAS 125850); tail smoothly tapering, with distinct whorls of scales; each transverse row of enlarged, pointed, oval, pointed, keeled tubercles separated by 3 rows of smaller scales; adjacent keeled dorsal caudal tubercles separated by $1-4$ rectangular to oval, smooth to very weakly keeled, smaller scales (a few tubercles in direct contact); subcaudal scales subimbricate; midventral caudal scales enlarged relative to adjacent scales (6-8 times size of dorsal caudal scales); 2 enlarged, pointed, dorsally-projecting postcloacal spurs on each side of tailbase, anterior
considerably larger than posterior.
Coloration (in preservative): Dorsum mid-brown with three faded grayish-brown transverse bands bordered by thinner dark brown edges. Anterior band extending from posteroventral border of orbit, through ear and across nape. Trunk band thinner, anterior to midbody, just posterior to position of elbow of adpressed forelimb. A third, broader pale band just anterior to hindlimb insertion is less conspicuous than the anterior bands. Dark anterior border of nape band passes through ventral portion of orbit to nostril; a cream band extending from anterodorsal margin of orbit to nostril. Top of head light brown with a slightly darker "V" shaped marking from supranasals to above anterior part of orbit; relatively symmetrical mid-brown markings at frontoparietal border and across mid-parietal table. Labials brown with areas of reduced pigment, especially around sutures and on posterior scales. Limbs slightly more yellowish than body dorsum. Tail relatively uniform grayishbrown with tubercles with white keels. Venter grayish-beige with very light, scattered brown pigment, densest along margins of flanks, limbs, and chin.

Variation.- Variation in mensural characters of the holotype and adult paratypes are presented in Table 5. Juvenile paratypes: CAS 125851: 26.8 mm SVL + 26.2 mm TailL; CAS 186287: 25.4 $\mathrm{mm}+25.0 \mathrm{~mm}$; CM 119310: $25.1 \mathrm{~mm}+26.4 \mathrm{~mm} ;$ CM 119311: $24.4 \mathrm{~mm}+21.4 \mathrm{~mm} ;$ NMNW R 10497: $26.0 \mathrm{~mm}+16.8 \mathrm{~mm}$. Dorsal scales much more strongly keeled in TM 54735 (Figs. 95-96), keels sharp, raised, caudal tubercles especially strongly keeled, either contacting adjacent tubercles or separated by a single narrow, elongate intervening scale. Paratypes with 4-5 lamellae under digits of manus and 5-6 under digits of pes. Dorsal pattern variable. CAS 186293 (Fig. 94) with interspaces between pale cross bands with vague, irregular linear patterns of yellowish-brown markings and limbs mottled; CM 119309 (Figs. 95, 97) similar but with a purplish brown base color and with original tail with weakly defined alternating pattern of light and mid-brown bands of approximately equal width - some lighter bands fused along dorsal midline, regenerated portion of tail more-or-less uniform mid-brown. CAS 125850-53 pattern largely faded to a uniform yellowish-brown, with paler nape and trunk bands, as well as pale sacral region visible in CAS 125851, more weakly expressed in larger specimens in this series. NMNW R 10496 with head dorsum yellowish brown and transverse bands relatively weakly developed, NMNW R 10498 with bands very inconspicuous, body soft, in poor condition. CM 119310-11, juveniles, with dark brown trunks with yellow-ish-brown presacral and sacral regions, hindlimbs and somewhat paler tail (Figs. 97-98). Narrow transverse trunk bands and well-demarcated nape band clearly visible. Top of head yellowishbrown, without markings. NMNW R 10497 with a dark band across pygal portion of tail, separating pale lumbosacral and postpygal regions. Adult paratype TM 54735 (Figs. 95-96) yellowishbrown with faded juvenile pattern. In life the juvenile color is blackish brown with a bright white trunk band, an ashy white nape band, and grayish-brown sacral area and hindlimbs. The top of the head is golden brown and the tail is a bright orange (Fig. 97; see also Seufer 1991). In life adult paratype CM 119309 had pinkish-gray bands and other markings on a yellowish brown dorsum, and white tipped tubercles (Fig. 97).

Distribution.- This species appears to be a Namibian endemic and has thus far been found at scattered localities in the Karasberge (Narudas), at Aroab on the western edge of the Kalahari, and along the Orange River between Sperlingsputs and Noordoewer (Figs. 21-22, 30).

Natural History. - At Narudas this species was collected under stones (Fig. 43). The habitat at Aroab is chiefly Kalahari sand and seems inappropriate for a member of the $P$. weberi group. However, there are scattered rocky areas in the vicinity and the types may have been collected in such a microhabitat. The few known localities for this species preclude a definitive characterization of its habitat type, but it has been found chiefly in smaller rock outcrops in the Orange River valley and the Karasberge (Figs. 99-100).

Conservation Status.- The species does not occur in any protected areas but is not under any specific threat.

## Pachydactylus carinatus Bauer, Lamb, and Branch, sp. nov.

Figures 101-105.
1966 [Pachydactylus serval] onscepensis [part] McLachlan and Spence, Ann. Cape Prov. Mus. 5:155. 1981 Pachydactylus serval onscepensis [part] Branch, Ann. Cape Prov. Mus. (Nat. Hist.) 13:145.
1988 Pachydactylus s. onscepensis [part] Branch, Field Guide:207.
1994 Pachydactylus s. onscepensis [part] Branch, Field Guide, 2 ${ }^{\text {nd }}$ ed.:207.
1998 Pachydactylus s. onscepensis[part] Branch, Field Guide, 3rd ed.:260, pl. 112, left middle.
2003 Pachydactylus cf. serval Bauer and Branch, Herpetol. Nat. Hist. 8:133.
2005 P[achydactylus]. serval [part] Bauer and Lamb, Afr. J. Herpetol. 54:116.
Type Material.- Holotype: CAS 201908 (Fig. 101): Adult female; South Africa, Northern Cape Province, Richtersveld National Park. 13.3 km E of Oenna Mine ( $28^{\circ} 05^{\prime} 11^{\prime \prime} \mathrm{S}, 17^{\circ} 07^{\prime} 45^{\prime \prime} \mathrm{E}$ ), coll. A.M. Bauer, 4 July 1996. Paratypes: CAS 201910 (Fig. 102): Adult male; South Africa, Northern Cape Province, Richtersveld National Park ( $28^{\circ} 02^{\prime} 41^{\prime \prime} \mathrm{S}, 17^{\circ} 05^{\prime} 40^{\prime \prime}$ E), coll. A.M. Bauer, 4 July 1996. CAS 201913 (Fig. 102): Adult male; South Africa, Northern Cape Province, Richtersveld National Park, 8.1 km S of Oenna Mine ( $28^{\circ} 06^{\prime} 40^{\prime \prime} \mathrm{S}, 17^{\circ} 01^{\prime} 10^{\prime \prime} \mathrm{E}$ ), coll.A.M. Bauer, 5 July 1996. CAS 203501: Adult male; South Africa, Northern Cape Province, Richtersveld National Park ( $28^{\circ} 02^{\prime} 41^{\prime \prime} \mathrm{S}, 17^{\circ} 05^{\prime} 40^{\prime \prime}$ ), coll. A.M. Bauer, 4 July 1996. CAS 203502: Adult male; South Africa, Northern Cape Province, Richtersveld National Park, 8.1 km S of Oenna Mine ( $28^{\circ} 06^{\prime} 40^{\prime \prime} \mathrm{S}, 17^{\circ} 01^{\prime} 10^{\prime} \mathrm{E}$ ), coll. A.M. Bauer, 5 July 1996. CAS 186340: Adult male; South Africa, Northern Cape Province, Richtersveld National Park, 20 km E Sendelingsdrif (2817Aa), coll. A.M. Bauer, 14 July 1992. PEM R 16629: Adult female; South Africa, Northern Cape Province, Richtersveld National Park, Hottentots Paradys Overlook (2816Bd), coll. W.R. Branch. TM 27949 (Fig. 102): Subadult male; South Africa, Northern Cape Province, 15 km NE Stinkfontein (2817Cd), coll. W.D. Haacke, H.D. Brown and W. Fürst, December 1962. Adult male; TM 34204, South Africa, Northern Cape Province, Richtersveld National Park, 2 mi E Swartpoort on Orange River ( 2816 Bb ), coll. W.D. Haacke, 24 September 1967. TM 81098: Adult male; South Africa, Northern Cape Province, Richtersveld National Park, Quiver Tree Camping Area (2817Ac), coll. M.J. Whiting and S.V. Nelson, August 1985.

Additional Material.- South Africa, Northern Cape Province: PEM R 224, CAS 231879-80*, 231881-82, Goodhouse (2818Cd); TM 34275, Devils Castle nr. Stinkfontein (2817Cd); TM 27943-48, 27950-52, 15 km NE Stinkfontein (2817Cd); TM 84535, 7 km from Lekkersing ( $29^{\circ} 00^{\prime} 43^{\prime \prime} \mathrm{S}$, $17^{\circ} 02^{\circ} 05^{\prime \prime}$ E); SAM 44700-01, 5 km E Vioolsdrif (2817Dd); TM 27963-68, 10 km S Vioolsdrif (2817Dd); TM 53839, Springbokvlakte ( $28^{\circ} 23^{\prime} \mathrm{S}, 17^{\circ} 14^{\prime} \mathrm{E}$ ); TM 27819 , 9 km from Annisfontein ( 2816 Bd ); SAM 43604, 43666, 45019-23, 45042, 45552-4, Annisfontein and vicinity (2816Bd); TM 27798, 10 km SW Annisfontein (2816Bd); TM 27808, Bloeddrif ( $28^{\circ} 21^{\prime}$ S, $16^{\circ} 49^{\prime}$ E); TM 45073, Rosyntjesberg, Richtersveld National Park (2817Cb); PEM R7363, just N Ochta Mine, Richtersveld National Park (2816Bb); CAS 200050*, LSUMZ $57292^{*}$, Rd. to Nicodaemus, 0.5 km from jct. Hottentotsparadys Lookout, Richtersveld National Park (2816Bd); TM 25139-41, 27824-25, Numees Mine ( $28^{\circ} 17^{\prime} \mathrm{S}, 16^{\circ} 58^{\prime} \mathrm{E}$ ); PEM R12560, Numees Spring, Richtersveld National Park ( $28^{\circ} 17^{\prime} 42^{\prime \prime}$ S, $16^{\circ} 58^{\prime} 05^{\prime \prime}$ E; TM 25159 , Cornelliskop ( $28^{\circ} 24^{\prime} \mathrm{S}, 16^{\circ} 53^{\prime} \mathrm{E}$ ); CAS 201922, 203504, Richtersveld National Park ( $28^{\circ} 19^{\prime} 12^{\prime \prime} \mathrm{S}, 16^{\circ} 58^{\prime} 30^{\prime \prime} \mathrm{E}$ ); TM 27833-35, Sendelingsdrif (2816Bb); TM 34203, 2 mi E Swartpoort, Richtersveld (2816Bb); PEM R 12550, Richtersveld National Park ( $28^{\circ} 05^{\prime} 59^{\prime \prime} \mathrm{S}$, $17^{\circ} 01^{\prime} 32^{\prime \prime} \mathrm{E}$ ); CAS $193365^{*}-67$, main park rd., 12.6 km E Sendelingsdrif, Richtersveld National Park (2816Bb); CAS 193374, 193392, main park rd., 22.8 km E Sendelingsdrif, Richtersveld National Park (2817Aa); CAS 193631-32, main park rd., 23.5 km E Sendelingsdrif, Richtersveld National Park (2817Aa); TM 84536-37, along Brown Pass after Halfmens Pass ( $28^{\circ} 10^{\prime} 38^{\prime \prime} \mathrm{S}, 17^{\circ} 01^{\prime} 53^{\prime \prime} \mathrm{E}$ ); CAS 200009, Swartpoort, Richtersveld National Park ( $28^{\circ} 03^{\prime} 59^{\prime \prime} \mathrm{S}, 16^{\circ} 58^{\prime} 37^{\prime \prime}$ E); TM 34205, 2 mi E Swartpoort on Orange River, Richtersveld National Park (2816Bb); CAS 201918, 2.7 km S of Oenna Mine, Richtersveld National Park ( $28^{\circ} 04^{\prime} 42^{\prime \prime} \mathrm{S}, 17^{\circ} 02^{\prime} 41^{\prime \prime} \mathrm{E}$ ); PEM R12547, 13.3 km E of Oenna Mine, Richtersveld National Park ( $28^{\circ} 05^{\prime} 11^{\prime \prime} \mathrm{S}$, $17^{\prime}\left(07^{\prime} 45^{\prime \prime}\right.$ E); PEM R12548, Richtersveld National Park ( $28^{\circ} 02^{\prime} 41^{\prime \prime} \mathrm{S}, 17^{\circ} 05^{\prime} 40^{\prime \prime} \mathrm{E}$ ); PEM R12544,

Sendelingsdrif Dump, Richtersveld National Park; PEM R7356, Akkedis Drive, Richtersveld National Park (2817Aa); LSUMZ 57293, Helskloof, Richtersveld National Park ( $28^{\circ} 19^{\prime} 46^{\prime \prime} \mathrm{S}, 16^{\circ} 59^{\prime} 25^{\prime \prime} \mathrm{E}, 695 \mathrm{~m}$ ); PEM R153, Tatasberg, Richtersveld National Park (2817Ad); PEM R1270, S Tatasberg, Richtersveld National Park ( 2817 Ac ); PEM R1960,Vandersterrberge, Richtersveld National Park (2817Ac); PEM R1960, $28^{\circ} 15^{\prime} 34^{\prime \prime}$ S, $17^{\circ} 08^{\prime} 19^{\prime \prime}$ E, Richtersveld National Park ( 2817 Ac ); PEM R12573, Kuboes Spring ( $28^{\circ} 26^{\prime} 36^{\prime \prime} \mathrm{S}, 16^{\circ} 59^{\prime} 36^{\prime \prime} \mathrm{E}$, 190 m ); PEM R11965, 2.3 km NE Geigas River junction on Kook River Spring Road ( $28^{\circ} 41^{\prime} 16^{\prime \prime} \mathrm{S}$, $17^{\circ} 07^{\prime} 44^{\prime \prime} \mathrm{E}, 440 \mathrm{~m}$ ); PEM R9244, Aramanshoek (2817Ca); SAM 45034-5, E Eksteenfontein near trig beacon 2605 ( 2817 Cd ); SAM 47724, Sabiesies ( $28^{\circ} 37^{\prime} 54^{\prime \prime}$ S, $17^{\circ} 00^{\prime} 43^{\prime \prime} \mathrm{E}$ ); CDNC 4845, Tierhoek, Ploegberg ( $28^{\circ} 37^{\prime} 54^{\prime \prime} \mathrm{S}, 17^{\circ} 00^{\prime} 43^{\prime \prime} \mathrm{E}$ ); TM 84537, Richtersveld National Park; TM 84537, Richtersveld; Namibia, Lüderitz District: TM 35383, Farm Spitskop (2716Dc); TM 35332, Farm Namuskluft (2716Dd); PEM R 12835, SAM 44435-36, Obib Mts. (2816Ba); TM 48351, Farm Plateau (2816); Karasburg District: JDV 2040, 62 km E Rosh Pinah (2817Aa); TM 28285-88, 28290, 28299, Fish River Canyon ( $27^{\circ} 35^{\prime} \mathrm{S}, 17^{\circ} 37^{\prime} \mathrm{E}$ ); TM 27978-81, Fish River Canyon ( $27^{\circ} 37^{\prime}$ S, $17^{\circ} 36^{\prime}$ E); TM 36825, Fish River Canyon National Park (2717Da); CAS 201875, Ai-Ais Nature Reserve, ca. 3 km N Orange River ( $28^{\circ} 12^{\prime} 26^{\prime \prime} \mathrm{S}, 17^{\circ} 16^{\prime} 43^{\prime \prime} \mathrm{E}$ ); JDV $3899,38 \mathrm{~km}$ E of water pump on Orange River [across from De Hoop] (2817Aa).

Etymology.- The specific epithet carinatus is Latin for keeled and is in reference to the prominent keeled tubercles typical of this species. The name is in the masculine form.

Diagnosis.- A moderately sized species, to 45.7 mm SVL (CAS 201908). Pachydactylus carinatus may be distinguished from all other members of the P. serval/weberi group by the combination of the following characters: snout weakly inflated laterally; rostral enters nostril; supranasals in variable contact; scales on dorsum of head granular, flattened to very weakly domed, those on snout much larger than those of interorbital and parietal regions; very few small (2-3 times size of granules), round, conical tubercles on interorbital and parietal regions; dorsal scalation strongly heterogeneous, with small, oval, keeled tubercles arranged in 16 regular rows; no tubercles on thighs; toes moderately long, toe pads relatively narrow; typically five undivided lamellae beneath digit IV of pes; tail to at least $114 \%$ of SVL, strongly annulate, bearing whorls of moderately to very strongly keeled, pointed tubercles, well separated from each other; adult pattern of moderately small, irregular brown spots or larger markings more-or-less evenly distributed across light brown to grayish-brown dorsum, with some trace of a pale, dark-edged band across occiput and nape in some specimens; tubercular keels whitish to pale yellow, contrasting with darker spots on dorsum (Figs. 101-103); juveniles with dark brown to blackish body, with an wide, dark-edged ashy nape band and an thick ashy band covering lumbar and sacral regions as well as hindlimbs (Figs. 104-105), tail a bright orange (Fig. 105; see also Bauer and Branch 2003:133). Although similar to the juvenile pattern of $P$. serval, in the latter species the tail is dark rather than bright, the pale sacral area extends further anteriorly than in $P$. carinatus and the neck band is also broader.

Description (based on holotype).- Adult female. Snout-vent length (SVL) 45.7 mm . Body relatively depressed, long (TrunkL/SVL ratio 0.44). Head elongate, large (HeadL/SVL ratio 0.30), relatively narrow (HeadW/HeadL ratio 0.61), somewhat depressed (HeadH/HeadL ratio 0.30), distinct from neck. Lores and interorbital region moderately inflated. Snout short (SnEye/HeadL ratio 0.33 ), longer than eye diameter ( $\mathrm{OrbD} / \mathrm{Sn}$-Eye ratio 0.74); scales on snout and forehead granular, round, flattened to slightly domed; scales on snout 2-3 times larger than those of anterior interorbital region, much larger than those of parietal table; a few small (2-3 times size of parietal granules) rounded, conical tubercles scattered on interorbital and parietal regions. Eye moderately large (OrbD/HeadL ratio 0.29); orbits without extra-brillar fringes; $1-3$ posterior supracilliary scales bearing very small spines; pupil vertical with crenelated margins. Ear opening oval, small (EarL/HeadL ratio 0.08), more-or-less vertically oriented; eye to ear distance less than diameter of eyes (EyeEar/OrbD ratio 0.91) [greater than eye diameter in some paratypes]. Rostral approximately $60 \%$ as deep ( 1.0 mm ) as wide (1.7); no rostral groove; contacted by two enlarged supranasals,
one small internasal granule, and first supralabials; nostrils oval, oriented laterally and slightly anteriorly, each surrounded by two postnasals, supranasal, and first supralabial; supranasals separated by a single small granule; dorsal postnasals approximately 1.5 times ventral postnasals, separated by two somewhat enlarged granules; nostril rims weakly inflated; 1-2 rows of scales separate orbit from supralabials; mental wedge-shaped, approximately 2.3 times deeper ( 2.0 mm ) than wide ( 0.8 mm ); no enlarged postmentals or chin shields. Supralabials to angle of jaws $11 / 10$ (9/9 to midorbit); infralabials 10/9; interorbital scale rows at midpoint of orbit 27 ( 9 across narrowest point of frontal bone).

Dorsal scales small, granular, flattened to weakly conical, forming rosettes of scales around moderately sized ( $6-8$ times size of adjacent scales), oval, relatively strongly keeled tubercles; tubercles largest on midflanks, smallest along dorsal midline and on anterior one third of body, arranged in 16 regular rows; ventral scales rounded, flattened, subimbricate to imbricate, becoming larger posteriorly, especially in precloacal region, approximately 24 between lowest rows of granular scales on flanks at midbody; scales on venter at midbody $1 / 3-1 / 2$ size of tubercles on dorsum at same level; chin granules approximately one third to one fourth size of ventral scales, increasing in size gradually on throat. No preanal or femoral pores. Scales on palm and sole granular to weakly conical; ventral surface of shank and forearm with smooth, subimbricating scales; preaxial surfaces of basal limb segments with smooth, slightly enlarged subimbricate to imbricate scales grading into juxtaposed granules on postaxial surfaces; scales on ventral aspect of thighs enlarged, continuous with enlarged scales of precloacal region.

Forelimbs moderately short, stout (ForeaL/SVL ratio 0.14); hindlimbs moderately long (CrusL/SVL ratio 0.17); digits moderately long, claws absent; subdigital scansors, except for distalmost, entire, present only on distal portion of toes, approximately 1.5 times wider than more basal (non-scansorial) subdigital scales; interdigital webbing absent. Relative length of digits (manus): $\mathrm{III}>$ IV $>$ II $>\mathrm{V}>$ I; (pes): $\mathrm{IV}>$ III $\sim \mathrm{V}>$ II $>$ I. Subdigital scansors (excluding small distal divided scansor) I (4), II (4), III (4), IV (4), V (4) - manus; I (4), II (5), III (6), IV (5), V (6) pes.

Tail sub-cylindrical, weakly depressed; partially regenerated tail equal to snout-vent length; tail thin basally, tapering, with distinct whorls of scales; each transverse row of oval, keeled tubercles separated by 3 rows of smaller, square to rectangular scales wit rounded free margins; subcaudal scales rectangular to oval, 2-3 times larger than dorsal caudal scales, imbricating; midventral caudal scales slightly larger than adjacent subcaudal scales; 2-3 small, raised, posterodorsally-projecting postcloacal spurs on each side of tailbase.

Coloration (in preservative): Dorsal color buff with small to moderately sized, evenly distributed mid-brown spots arranged in more-or-less longitudinal rows. A pale, wide, transverse band across nape, bordered anteriorly and posteriorly by a incomplete thin mid-brown edge. Keels of tubercles whitish to cream, contrasting with underlying brown spots. Parietal table, interorbital area and snout with symmetrical brown spots: a triangle pointing forward fro anterior border of orbits, a small rhomboid on anterior part of parietal table, surrounded by a roughly star-shaped brown outline. A brown line from rostral, through center of eye, over ear to level of dark anterior border of nape band, widened medially in the region to approach dorsal midline on the snout. First supralabial scales midbrown; more posterior supralabials and all infralabials buff tinged with brown pigment. Limbs with scattered irregular mid-brown spots and blotches. Tail with alternating light and dark bands; cream bands wider than dark bands, becoming subequal distally. Tail tubercles whitish. Venter buff with scattered diffuse pigmentation, especially on edges of flanks and chin and under limbs. Tail venter with faint alternating pattern.

Variation.- Variation in mensural characters of the holotype and adult paratypes are present-
ed in Table 6. Tail length is a maximum of $114 \%$ of SVL in TM 27949 (Fig. 102). Dorsal tubercle size and keeling vary considerably. Tubercles are especially small in TM 27949. Supralabial contact varies among the paratypes. Small claws are present on at least some specimens. Most paratypes with only 5 subdigital lamellae under digits II-V of pes. Adult color pattern variable. Nape band very well defined in TM 34204 and TM 27949. Dorsal pattern with large blotches instead of smaller spots in CAS 186340 and CAS 201910. Hatchlings (TM 25139 - 18.1 mm SVL, CAS 193367-19.7 mm SVL) dark brown with a wide pale neck band with dark edges (Fig. 104). A pale patch on sacral and presacral regions, also bordered by dark edges. In specimens as small as 20.71 mm (CAS 193374) the dark dorsal background color fades and spots become evident, with the light sacral-presacral area becoming obscured. Nape band remains bold in specimens up to approximately 34 mm SVL, then is variably distinct in larger specimens.

Distribution.- This species is distributed throughout the Richtersveld National Park and in adjacent parts of southern Namibia (Figs. 21, 30-31). It occurs in areas along the Orange River both to the east and west of the park boundaries - Annisfontein in the west and several localities in the east, at least as far upstream as Goodhouse, where it is replaced by P. montanus. It extends southwards to about the level of Kuboes and northwards as far as Namuskluft in the west and Ai-Ais in the east. Pachydactylus carinatus occurs sympatrically with P. montanus at several localities between Goodhouse and the Rosh Pinah area and with P. serval in the Fish River Canyon. Several specimens (TM 36783-85) from Farm Koboop (Coboboop) (2819Cd) on the south bank of the Orange River near Onseepkans (Fig. 30) are superficially similar to P. carinatus. Their identity remains uncertain, although it is possible that they could represent an easternmost locality for this species.

Natural History.- In most of its area of distribution, $P$. carinatus is rupicolous and occupies retreats under overhanging rock flakes and narrow cracks and crevices within and between rocks in bouldery areas (Figs. 106-107); however, along the Orange River it has been found on the ground under stones or refuse (Figs. 88-89; Bauer and Branch 2003). It has been found from about 40 m above sea level near the Orange River to approximately 720 m above Helskloof Pass.

Conservation Status. - This species is widely distributed in largely uninhabited areas. Most of its range is encompassed by the Ai-Ais/Richtersveld Transfrontier Park.

Remarks.- Bauer and Branch (2003) first signaled the distinctiveness of this form.

## Pachydactylus visseri Bauer, Lamb, and Branch, sp. nov.

Figures 108-111.
1988 Pachydactylus weberi [part] Branch, Field Guide:208, pl. 86, lower middle left.
1994 Pachydactylus weberi Branch, Herpetol. Nat. Hist. 2:2.
1994 Pachydactylus weberi [part] Branch, Field Guide, 2nd ed.:208, pl. 86, lower middle left.
1998 Pachydactylus weberi [part] Branch, Field Guide, 3rd ed.:263, pl. 86, lower middle left.
2003 Pachydactylus cf. weberi [part] Bauer and Branch, Herpetol. Nat. Hist. 8:134.
2005 P[achydactylus]. weberi [part] Bauer and Lamb, Afr. J. Herpetol. 54:116.
Type Material.- Holotype: CAS 201874 (Fig. 108): Adult male; Namibia, Karas Region, Karasburg District, Ai-Ais Nature Reserve. c. 3 km N Orange River ( $28^{\circ} 12^{\prime} 26^{\prime \prime} \mathrm{S}, 17^{\circ} 16^{\prime} 43^{\prime \prime} \mathrm{E}$ ), coll. A.M. Bauer. 26 June 1996. Paratypes: TM 28289: Adult male: Namibia, Karas Region, Karasburg District, Fish River Canyon viewpoint ( $27^{\circ} 35^{\prime}$ S. $17^{\circ} 37^{\prime}$ E), coll. W.D. Haacke. December 1962. TM 35455-56 (Fig. 109): Adult females: Namibia, Karas Region. Lüderitz District, 10 mi. NW Fish River Mouth (2817Aa) [locality given in collection database as Kuamsib Mountain. $27^{\circ} 59^{\prime} \mathrm{S}$, $17^{\circ} 05^{\prime} \mathrm{E}$ ]. coll.W.D. Haacke, 23 September 1968. TM 35363: Adult male: Namibia. Karas Region, Lüderitz District. Farm Namuskluft (2716Dd), coll. unknown: TM 57399: Adult female; Namibia. Karas Region. Karasburg District. Fish River Canyon viewpoint
( $27^{\circ} 35^{\prime}$ 'S. $17^{\circ} 37^{\prime}$ E), coll. W.D. Haacke, February 1984. TM 50110 (Fig. 109): Adult male; Namibia, Karas Region, Karasburg District, Ai-Ais (2717Dd), coll.F. Odendaal, May 1977. NMNW R 8979: Adult male; Namibia, Karas Region, Lüderitz District, Rooilepel ( $28^{\circ} 14^{\prime} 51^{\prime \prime} \mathrm{S}$, $16^{\circ} 39^{\prime} 31^{\prime \prime} \mathrm{E}$ ), on upper slopes, 500 m , coll.W.R. Branch.

Additional Material.- South Africa, Northern Cape Province: PEM R 12804, Kubus (2816Bd); TM 35256, Brandkaross (2816Bc); TM 84560-62, Farm Richtersveld 11, between Baken and Bloeddrif along S bank of Orange R. ( $28^{\circ} 22^{\prime} 07^{\prime \prime} \mathrm{S}, 16^{\circ} 48^{\prime} 19^{\prime \prime} \mathrm{E}$ ); TM 27836-37, Sendelingsdrif, Richtersveld National Park (2816Bb). Namibia, Lüderitz District: CAS 201899, PEM R 7395-96, Skilpadberg, Sperrgebiet ( $28^{\circ} 27^{\prime} 43^{\prime \prime} \mathrm{S}$, $16^{\circ} 40^{\prime} 05^{\prime \prime}$ E); [?] PEM R 7408-10, Rooilepel ( $28^{\circ} 14^{\prime} 51^{\prime \prime} \mathrm{S}, 16^{\circ} 39^{\prime} 31^{\prime \prime} \mathrm{E}$ ); TM 35440 , 10 mi . NW Fish River Mouth (2817Aa); [?] PEM R 7434-36, E slopes Aurusberg ( $27^{\circ} 38^{\prime} 55^{\prime \prime} \mathrm{S}$, $16^{\circ} 20^{\prime} 07^{\prime \prime} \mathrm{E}$ ); [?] PEM R 7441, 7449 , NE slopes Aurusberg ( $27^{\circ} 38^{\prime} \mathrm{S}, 16^{\circ} 20^{\prime} \mathrm{E}$ ); TM 27750, Signalberg, Auros Mts. ( $27^{\circ} 43^{\prime} \mathrm{S}$, $16^{\circ} 17^{\prime}$ E); JDV 3903, just S Aus (2616Cb); Karasburg Distirct: PEM R 4825, Ai-Ais (2717Dd); PEM R 4638, 4658, Fish River Canyon (2717Da); CAS 201877, Ai-Ais Nature Reserve, 82.4 km W Noordoewer ( $28^{\circ} 11^{\prime} 07^{\prime \prime} \mathrm{S}, 17^{\circ} 14^{\prime} 58^{\prime \prime} \mathrm{E}$ ); NMNW 8854-55, Ai-Ais Nature Reserve, c. 3 km N Orange River ( $28^{\circ} 12^{\prime} 26^{\prime \prime} \mathrm{S}$, $17^{\circ} 16^{\prime} 43^{\prime \prime} \mathrm{E}$ ).

Etymology.- The specific epithet is a patronym honoring John D. Visser, an important contributor to southern African herpetology who kindly provided several hundred specimens from his personal collection for use in this study. The name is constructed in the masculine genitive. The epithet also reflects the occurrence of the species in the Fish (Vis) River Valley.

Diagnosis.- A relatively large species, to 48.5 mm SVL (PEM R 4638). Pachydactylus visseri may be distinguished from all other members of the $P$. serval/weberi group by the combination of the following characters: nasal region not inflated; rostral excluded from nostril; supranasals in broad or narrow contact; scales on snout and canthus granular, rounded to oval, flattened to weakly domed, much larger than granular scales of interorbital and parietal regions; small, rounded, conical tubercles, much smaller than snout scales, interspersed among granules of interorbital and parietal regions; dorsal scalation heterogeneous, with moderately large ( $6-9$ times dorsal granules), oval, distinctly keeled arranged in 16-18 regular rows, largest on midflanks; thighs bearing enlarged keeled tubercles; toes relatively short, toe pads relatively narrow; typically five undivided lamellae beneath digit IV of pes; tail to at least $120 \%$ of SVL, annulate, bearing whorls of moderately large, pointed, weakly to strongly keeled tubercles; adult pattern a series of distinct, wide, pale (cream to beige) transverse bands separated by thinner dark brown bands. Six bands (rarely seven) anterior to sacrum (one on nape, one across shoulders, four evenly spaced between axilla and hindlimb insertion); tail with strongly contrasting cream and dark brown bands of approximately equal width (Figs. 109-110). Juvenile pattern similar to adult (Fig. 111).

DESCRIPTION (based on holotype). - Adult male. Snout-vent length (SVL) 38.6 mm . Body relatively depressed, relatively long (TrunkL/SVL ratio 0.45). Head elongate, large (HeadL/SVL ratio 0.32 ), narrow (HeadW/HeadL ratio 0.59), moderately depressed (HeadH/HeadL ratio 0.36), distinct from neck. Lores and interorbital region moderately inflated. Snout short (Sn-Eye/HeadL ratio 0.34 ), much longer than eye diameter (OrbD/Sn-Eye ratio 0.72); scales on snout and forehead smooth, flattened to weakly domed; large on snout and canthus becoming granular on interorbital region with larger (3-4 times parietal granules) weakly conical tubercles interspersed; scales on snout much larger (5-10 times parietal granules). Enlarged ( $2-3$ times parietal tubercles), conical tubercles regularly scattered across temporal region and occiput, as far posterior as nape. Eye moderately small (OrbD/HeadL ratio 0.24 ); orbits without extra-brillar fringes; 5 supracilliary scales at posterodorsal corner of orbit bearing very small spines; pupil vertical, with crenelated margins. Ear opening oval, vertically oriented, small (EarL/HeadL ratio 0.07); eye to ear distance slightly greater than diameter of eyes (EyeEar/OrbD ratio 1.05). Rostral approximately $50 \%$ as deep ( 0.7 mm ) as wide (1.4), no rostral groove, contacted by two enlarged supranasals and first supralabials; nostrils
oval, oriented laterally, each surrounded by two postnasals, supranasal, and first supralabial; supranasals in contact anteriorly, separated by a single granule posteriorly; dorsal postnasals larger than ventral postnasals, separated by 3 granules; nostril rims not inflated, bordered posteriorly by a slight depression; one row of scales separate orbit from supralabials; mental wedge-shaped, tapering posteriorly, approximately 2.2 times deeper ( 1.7 mm ) than wide ( 0.8 mm ); no enlarged postmentals or chin shields. Supralabials to angle of jaws 11/11 (8/9 to mid-orbit); infralabials 9/9; interorbital scale rows at midpoint of orbit 25 ( 7 across narrowest point of frontal bone).

Dorsal tubercles large ( $8-10$ times size of adjacent scales), largest on midflanks and smallest along dorsal midline and on anterior one third of trunk, oval, with a pronounced median keel, forming 18 regular longitudinal rows on trunk; each tubercle surrounded by rosette of small granular scales; ventral scales flattened, oval subimbricate to imbricate, becoming larger posteriorly, largest on posterior abdomen and in precloacal region, approximately 35 between lowest granular rows on flank at midbody; tubercular scales on dorsum at midbody larger than ventral scales at same level; chin granules approximately one third to one fourth size of ventral scales, increasing in size gradually on throat. No preanal or femoral pores. Scales on palm, sole, and ventral surface of forelimb smooth, granular; scales on ventral aspect of hindlimbs enlarged, continuous with enlarged scales of precloacal region; scales on dorsal aspect of forelimb smooth, subimbricate proximally, with small conical tubercles intermixed among more strongly imbricate scales distally; scales on dorsum of thigh and crus greatly enlarged, strongly keeled.

Forelimbs moderately long, stout (ForeaL/SVL ratio 0.15); hindlimbs long (CrusL/SVL ratio 0.18 ); digits relatively short, claws absent; subdigital scansors, except for distalmost, entire, present only on distal portion of toes, approximately 1.5 times wider than more basal (non-scansorial) subdigital scales; interdigital webbing absent. Relative length of digits (manus): III $>$ IV $>$ II $>\mathrm{V}>$ I; (pes): IV $>$ III $\sim$ V $>$ II $>$ I. Subdigital scansors (excluding small distal divided scansor) I (3), II (4), III (4), IV (4), V (4) - manus; I (3), II (4), III (5), IV (5), V (5) - pes.

Tail (based on paratypes) sub-cylindrical, depressed; original tail longer than snout-vent length (TailL/SVL ratio 1.20; based on TM 35455); tail relatively thin basally, tapering, with distinct whorls of scales; each transverse row of enlarged, oval, pointed, strongly keeled tubercles separated by 3 rows of smaller scales; adjacent keeled dorsal caudal tubercles generally separated by a single smaller scale; subcaudal scales rhomboidal to pentagonal, imbricating; midventral caudal scales enlarged relative to adjacent scales ( $10+$ times size of dorsal caudal scales); two enlarged, pointed, posterodorsally-projecting postcloacal spurs on each side of tailbase, anterior considerably larger than posterior.

Coloration (in life): Dorsum with alternating pale (cream to beige with pinkish tinge) and dark (mid-brown with darker margins) transverse bands, pale bands wider than dark, narrowing on flanks. Anterior most band across nape, second over shoulders, four remaining bands evenly distributed between axilla and hindlimb insertion. A mid-brown streak extending from nostril through middle of orbit and above ear to occiput, forming anterior border of pale nape band; a second, more diffuse brown stripe from labials, through ear to meet posterior dark border of pale nape band. Snout with diffuse, symmetrical brown markings, fading in interorbital region; diffuse brown markings over center of parietal table. Labials white with mid-brown pigment extensive on posterior labials, anteriormost labials with pigment limited to center of scales. Forelimbs relatively uniform light brown; hindlimbs with diffuse mid-brown barring basally. Tail (based on TM 35455) with alternating light (light brown or beige basally, cream to whitish distally) and dark (mid- to dark brown) bands of approximately equal width. Venter beige to cream, unpigmented except for scattering of fine brown speckles under limbs and at edges of chin and flanks.

Variation.- Variation in mensural characters of the holotype and most paratypes are present-
ed in Table 7 (measurements of juvenile paratype, CAS 201877, 24.2 mm SVL, not provided). The paratypes exhibit moderate variation in the degree of supranasal contact, degree of tubercle keeling, and labial counts. Coloration is very consistent across paratypes, including juvenile specimen. Specimens from the Orange River significantly below the Fish River confluence vary in pattern. Seven pale bands are present on the dorsum of TM 27836-37, from Sendelingsdrif. In TM 84560-61 and CAS 201899 the bands posterior to the nape are more diffuse and angled rather than transversely oriented.

Distribution.- This species is distributed throughout the Richtersveld and adjacent parts of southern Namibia, including the Fish River Canyon (Fig. 89), the Aurusberg, and near Aus (Figs. 21-22, 30; see Remarks). Branch (1994b) considered that its distribution in the Sperrgebiet of southern Namibia was limited by humidity requirements to only a few more mesic localities. Although broadly sympatric with P. monicae, P. visseri ranges farther northward and westward.

Natural History.- Branch (1994b) found this species (as P. weberi) sheltering in cracks on a limestone outcrop at Skilpadberg (Fig. 112) and under exfoliating flakes of granite in the Aurusberg. He considered it likely that the species requires a relatively mesic microclimate, thus limiting its distribution in the Sperrgebiet. Branch (1994b) reported egg size of one clutch as 10.3 $\times 7.2 \mathrm{~mm}, 0.2 \mathrm{~g}$ and $9.7 \times 7.3 \mathrm{~mm}, 0.2 \mathrm{~g}$.

Conservation Status.- This species is distributed chiefly in uninhabited regions and does not appear to be under any particular threats. Most of its range occurs within the AiAis/Richtersveld Transfrontier Park and the Sperrgebiet.

Remarks.- Specimens from the Aurusberg are tentatively referred to this species, but these animals typically have a more irregular dorsal pattern than those from the remainder of the range and require further study. Unfortunately no genetic material was available for these populations. A single specimen from "just south of Aus" (JDV 3903) would appear to be well out of the core range of the species. It is unclear if additional isolated populations occur in suitably rocky intervening areas of the Sperrgebiet, such as the Klinghardt Mountains.

## Pachydactylus goodi Bauer, Lamb, and Branch, sp. nov.

Figures 113-116.
2005 P[achydactylus]. weberi [part] Bauer and Lamb, Afr. J. Herpetol. 54:116.
Type Material.- Holotype: TM 27962 (Fig. 113): Adult male; South Africa, Northern Cape Province, 10 km S Vioolsdrif (2817Dc), coll. W.D.Haacke, December 1962. PARATYPES: TM 29707 (Fig. 116): Juvenile; South Africa, Northern Cape Province, 10 km S Vioolsdrif (2817Dc), coll. W.D. Haacke, December 1962. TM 84505 (Fig. 114): Adult female; South Africa, Northern Cape Province, Farm Aggenys 56 ( $29^{\circ} 12^{\prime} 26^{\prime \prime} \mathrm{S}, 18^{\circ} 50^{\prime} 44^{\prime \prime}$ E), coll. E. Scott, 19 February 2003. CAS 231878 (Figs. 114-115): Adult male; South Africa, Northern Cape Province, 77 km E Springbok (2918Bc), coll. J.D. Visser, 13 September 1980.

Etymology.- The specific epithet is a patronym honoring our friend and colleague David A. Good who, with the first and third authors, performed a herpetofaunal survey of the Richtersveld and collected much of the material of the $P$. weberi group from along the lower Orange Valley during the mid-1990s. The name is constructed in the masculine genitive.

Diagnosis.-A large species, to 50.0 mm SVL. Pachydactylus goodi may be distinguished from all other members of the P. serval/weberi group by the combination of the following characters: nasal region not strongly inflated laterally; rostral excluded from nostril; supranasals in contact anteriorly; scales on snout and canthus flattened to weakly domed, those of interorbital and parietal regions tiny, granular, with larger, rounded, conical tubercles interspersed; scales on snout equal to or greater than size to interorbital tubercles; dorsal scalation heterogeneous, with relative-
ly large, oval, strongly keeled tubercles arranged in approximately $16-18$ regular rows; large keeled to mucronate tubercles on thighs; toes relatively short, toe pads relatively narrow; five undivided lamellae beneath digit IV of pes; tail to at least $113 \%$ of SVL, annulate, bearing whorls of large, pointed, strongly keeled tubercles, separated from each other by a single, narrow scale row; adult pattern chocolate to purplish-brown with a series of three very bold, white, complete transverse bands with well-defined, thick, dark brown margins: one from posteroventral margin of orbits across nape, one at mid-body and one presacral; white markings also present on the dorsum of thighs and on proximal forelimbs and forelimb insertions; tail with alternating mid-brown and white to cream, dark edged bands (Figs 113-115); juvenile pattern as adult (Fig. 116).

Description (based on holotype). - Adult male. Snout-vent length (SVL) 50.0 mm . Body relatively depressed, relatively short (TrunkL/SVL ratio 0.41). Head elongate, large (HeadL/SVL ratio 0.28 ), wide (HeadW/HeadL ratio 0.71 ), not strongly depressed (HeadH/HeadL ratio 0.43 ), distinct from neck. Lores and interorbital region weakly inflated. Snout long (Sn-Eye/HeadL ratio 0.40), much longer than eye diameter (OrbD/Sn-Eye ratio 0.68 ); scales on snout and forehead smooth, domed; large on snout and canthus becoming granular on interorbital region, with larger, weakly conical tubercles interspersed; scales on snout much larger than those of parietal table. Enlarged, weakly conical tubercles regularly scattered across interorbital, parietal, and temporal regions as far posterior as nape. Eye moderately large (OrbD/HeadL ratio 0.27); orbits without extra-brillar fringes; 5-6 supracilliary scales at posterodorsal corner of orbit bearing small spines; pupil vertical, with crenelated margins. Ear opening rounded, moderately large (EarL/HeadL ratio 0.09); eye to ear distance greater than diameter of eyes (Eye-Ear/OrbD ratio 1.13). Rostral approximately 45\% as deep $(0.8 \mathrm{~mm})$ as wide ( 1.8 ), no rostral groove, contacted by two enlarged supranasals and first supralabials; nostrils oval, oriented laterally and slightly dorsally, each surrounded by two postnasals, supranasal, and narrowly by first supralabial; supranasals in contact anteriorly, separated by a single granule posteriorly; dorsal postnasals larger than ventral postnasals, separated by $2-3$ granules; nostril rims weakly inflated, bordered posteriorly by a distinct notch or pit; one row of scales separate orbit from supralabials; mental with nearly parallel sides, tapering only slightly posteriorly, approximately 2.3 times deeper ( 2.2 mm ) than wide ( 1.0 mm ); no enlarged postmentals or chin shields. Supralabials to angle of jaws 11/10 (9/9 to mid-orbit); infralabials 9/8; interorbital scale rows at midpoint of orbit 27 ( 7 across narrowest point of frontal bone).

Dorsal tubercles large ( $10-12$ times size of adjacent scales), largest on dorsolateral surfaces and smallest along dorsal midline, rounded, with a pronounced median keel, forming 18 longitudinal rows on trunk; each tubercle surrounded by rosette of small granular scales; ventral scales flattened, subimbricate, becoming larger posteriorly, approximately 46 between lowest tubercular rows at midbody; tubercular scales on dorsum at midbody much larger than those on venter at same level; chin granules approximately one third to one fourth size of ventral scales, increasing in size rather abruptly on throat. No preanal or femoral pores. Scales on palm, sole, and ventral surface of forelimb smooth, granular; scales on ventral aspect of hindlimbs enlarged, continuous with enlarged scales of precloacal region; scales on dorsal aspect of forelimb smooth proximally, with small conical tubercles intermixed distally; scales on dorsum of thigh and crus greatly enlarged, conical or strongly keeled.

Forelimbs moderately short, stout (ForeaL/SVL ratio 0.14 ); hindlimbs moderately long (CrusL/SVL ratio 0.18); digits relatively short, claws absent; subdigital scansors, except for distalmost, entire, present only on distal portion of toes, 1.2-1.5 times wider than more basal (non-scansorial) subdigital scales: interdigital webbing absent. Relative length of digits (manus): III > IV > II $>$ V $>$ I: (pes): IV $>$ III $\sim$ V $>$ II $>$ I. Subdigital scansors (excluding small distal divided scansor) I (4), II (4), III (4), IV (4), V (4) - manus; I (4), II (5), III (5), IV (5), V (5) - pes.

Tail sub-cylindrical, very slightly depressed; partially regenerated tail shorter than snout-vent length (TailL/SVL ratio 1.12); tail relatively thin basally, tapering, with distinct whorls of scales; each transverse row of enlarged, pointed, strongly keeled tubercles separated by 3-4 rows of smaller scales: adjacent keeled dorsal caudal tubercles separated by a single narrow, elongate scale; subcaudal scales imbricating; midventral caudal scales enlarged (5-7 times size of dorsal caudal scales); two enlarged, pointed, posterodorsally-projecting postcloacal spurs on each side of tailbase.

Coloration (in preservative): Dorsum purplish-brown with a bold pattern of three beige transverse bands with thick, well-defined dark brown borders. Anterior band extending from orbit to orbit across occiput and nape. Light portion of band continuous with pale labial scales; dark anterior margins of band continue through orbit to nostrils, becoming lighter on snout. Second band at midbody, third in presacral position. Top of head uniform yellowish-mid-brown with pair of welldefined pale stripes from anterior of orbit to postnasal scales. Forelimbs uniform purplish-brown; hindlimbs purplish-brown with a single dark edged pale band on thigh, continuous with presacral trunk band when limbs are protracted. Original portion of tail with bold alternating pattern of pur-plish-brown and dark-edged cream bands of approximately equal size; regenerated portion of tail uniform purplish-brown. Venter grayish-cream, unpigmented.

Variation.- Variation in mensural characters of the holotype and paratypes are presented in Table 8. Paratypes TM 84505 (Fig. 114) and CAS 231878 (Figs. 114-115) have a similar pattern to the holotype, but have less faded colors, the dominant dorsal color is light to mid-brown, whereas the light bands are white, rather than cream. TM 84505 lacks the band on the thigh. Juvenile paratype TM 29707 (Fig. 116; SVL 18.8) has extensive skin and forelimb damage. Its dorsal pattern is similar to the adult pattern, but the dark brown borders of the white bands are not as strongly contrasting with the mid-brown dorsal coloration as in the adults. In life, the purplish dorsal color is a chocolate brown, the pale bands are bright white, and there are white markings on the dorsal surfaces of the thighs and of the forelimbs (Fig. 115).

Distribution.- This species has been found at several localities across the extreme north of the Northern Cape Province of South Africa, between Vioolsdrif and Aggenys (Figs. 21-22, 30), but has not been found on the Namibian side of the Orange River. Its distribution thus complements that of the similar P. mclachlani.

Natural History. - Nothing is known of the natural history of this species.
Conservation Status.- This species has a restricted range and its habitat requirements are unknown. It does not occur in any protected areas and should be considered vulnerable.

Remarks. - No tissue samples were available from this species, but based on purely phenetic grounds, it would appear to be most closely related to P. mclachlani.

## Pachydactylus otaviensis Bauer, Lamb, and Branch, sp. nov.

Figures 117-118.
1984 Pachydactylus weberi [part] Visser, Landbouweekbl. 27 April 1984:53.
2005 P[achydactylus]. weberi [part] Bauer and Lamb, Afr. J. Herpetol. 54:116.
Type Material. - Holotype: TM 45097 (Fig. 117): Adult male; Namibia, Oshikoto Region, Tsumeb District, Farm Uithoek (1917Bc), coll. G. Voigt, 29 April 1974. PARATYPEs: TM 85000 (Fig. 118): Adult male, TM 85002 (Fig. 118): Juvenile; Namibia, Oshikoto Region, Tsumeb District, Farm Varianto (on Elandshoek) ( $19^{\circ} 22^{\prime} 46^{\prime \prime} \mathrm{S}, 17^{\circ} 44^{\prime} 27^{\prime \prime} \mathrm{E}$ ), coll. E. Scott, 4 January 2004.

Etymology.- Named for the Otaviberge or Otavi Highlands, a low range of dolerite hills in northeastern Namibia to which this species appears to endemic.

Diagnosis. - Snout-vent length to at least 42.9 mm (TM 85000). May be distinguished from
all other members of the $P$. serval/weberi group by the combination of the following characters: snout blunt; rostral excluded from nostril; supranasals in narrow anterior contact; scales on dorsum of head weakly conical, those on snout much larger than those of interorbital region; interorbital and parietal granules intermixed with scattered, conical tubercles, each smaller than scales of snout; dorsal scalation heterogeneous, consisting of small conical scales interspersed with larger strongly keeled to mucronate tubercles; tubercles becoming conical on flanks; tubercles in 18 rows; thighs bearing very large conical tubercles; toes moderately long, toe pads relatively narrow; five undivided lamellae beneath digit IV of pes; tail (partly regenerated) to at least $102 \%$ of SVL, annulate, bearing whorls of large, pointed, strongly keeled tubercles, narrowly separated from each other; cloacal spurs very large bearing dorsally-directed pointed scales with concave surfaces; adult pattern of three pale bands (nape, just posterior to adpressed elbow, and posterior trunk, anterior to lumbar region) separating broader areas of grayish-brown with darker brown edges - pattern may be obscured and appear as 5-6 dark brown bands on a pale background (Figs. 117-118); juvenile pattern as adult, with three pale bands (Fig. 118).

Description (based on holotype).- Adult male. Snout-vent length (SVL) 39.4 mm. Body relatively depressed, short (TrunkL/SVL ratio 0.40). Head elongate, large (HeadL/SVL ratio 0.30), relatively wide (HeadW/HeadL ratio 0.65), not strongly depressed (HeadH/HeadL ratio 0.42), distinct from neck. Lores and interorbital region inflated. Snout short (Sn-Eye/HeadL ratio 0.39), longer than eye diameter (OrbD/Sn-Eye ratio 0.66); scales on snout and forehead granular to conical, round to oval; scales on snout much larger than those of parietal table. Eye moderately large (OrbD/HeadL ratio 0.26 ); orbits without extra-brillar fringes; posterior supracilliary scales bearing small spines; pupil vertical,with crenelated margins. Ear opening oval, small (EarL/HeadL ratio 0.07 ), greatest diameter vertical; eye to ear distance much greater than diameter of eyes (EyeEar/OrbD ratio 1.51). A series of enlarged conical tubercles between posterior border of orbit and occiput. Rostral approximately $60 \%$ as deep ( 1.0 mm ) as wide (1.6); no rostral groove; contacted by two enlarged supranasals and first supralabials; nostrils oval, each surrounded by two postnasals, supranasal, and first supralabial; supranasals in narrow contact anteriorly, separated posteriorly by a single granule; dorsal postnasals separated by three granules; nostril rims weakly inflated; one row of scales separate orbit from supralabials; mental wedge-shaped, approximately 1.8 times deeper $(1.7 \mathrm{~mm})$ than wide $(1.0 \mathrm{~mm})$; no enlarged postmentals or chin shields; Supralabials to angle of jaws 10 (8 to mid-orbit); infralabials 9 ; interorbital scale rows (at midpoint of orbit) 23 (11 across narrowest point of frontal bone).

Scales of snout much larger than those of forehead; scales grade from conical on parietal region to keeled or mucronate on nape; dorsal tubercles large (4-6 times size of adjacent scales), rounded, with a pronounced median keel and obliquely-oriented ridges laterally, forming approximately 18 rows; tubercles largest on mid-flanks, keels somewhat flattened over sacrum; each enlarged tubercle surrounded by rosette of smaller scales; ventral scales flattened, subimbricate, becoming somewhat larger posteriorly, approximately 38 between lowest tubercular rows at midbody; scales on dorsum at midbody much larger than those on ventrum at same level; chin granules approximately one half size of ventral scales, increasing gradually in size on throat. No preanal or femoral pores. Scales on palm, sole, and ventral surface of forelimb smooth, granular; scales on ventral aspect of hindlimbs enlarged. juxtaposed to subimbricate; scales on dorsal aspect of forelimb smooth proximally, with small conical tubercles intermixed distally; scales on dorsum of thigh and crus greatly enlarged, conical or keeled to mucronate, terminating in sharp points.

Forelimbs moderately short, stout: forearm short (ForeaL/SVL ratio 0.14 ); hindlimbs relatively short, tibia moderately short (CrusL/SVL ratio 0.17); digits relatively short, claws absent; subdigital scansors. except for distalmost, entire, present only on distal portion of toes, 1.5-2.0 times
wider than more basal (non-scansorial) subdigital scales; interdigital webbing absent. Relative length of digits (manus): III $>$ IV $>$ II $>$ V $>$ I; (pes): IV $>$ III $\sim$ V $>$ II $>$ I. Subdigital scansors, exclusive of divided distalmost scansor (manus): I (4), II (4), III (4), IV (4), V (4); (pes) I (4), II (5), III (5), IV (5), V (5).

Tail sub-cylindrical, somewhat depressed; partially regenerated tail longer than snout-vent length (TailL/SVL ratio 1.02); tail relatively thick basally, tapering, with distinct whorls of scales; each transverse row of enlarged, keeled tubercles separated by $2-3$ rows of smaller scales; smaller scale rows continuous around tail; each row of enlarged tubercles replaced ventrally by two rows of smaller scales; each row of keeled dorsal caudal tubercles interrupted occasionally by $1-2$ small granules; subcaudal scales pointed posteriorly, subimbricating; four greatly enlarged, pointed, concave, dorsally-projecting postcloacal spurs on each side of tailbase, subtended by two smaller rows of dorsolaterally projecting pointed scales.

Coloration (in preservative): Ground color of dorsum beige to light brown with six mid-brown cross bands: one behind light nape band, four on trunk on one on sacrum. Lateral surface of head with dark brown streak from nostril and anterior supralabials through eye and above ear, fusing with opposite side on nape to form anteriormost dark cross marking; dark V-shaped mark diverging from supranasal scales to dorsal aspects of orbits; scattered dark markings on frontal and parietal regions; diffuse, partly broken dark line from angle of jaws to retroarticular process. Limbs mottled, with light and dark markings roughly alternating. Tail banded with 13 somewhat irregular narrower dark bands alternating with lighter interstices. Venter beige with scattered dark punctuations, especially on scales near edges of flanks and under limbs and tail.

Variation.- Variation in mensural characters of the holotype and paratypes are presented in Table 9. Adult paratype (TM 85000) similar in scalation to holotype, including distinctive cloacal spurs. Tail broader and more depressed. Banding more distinctive, with clearly demarcated nape band and two trunk bands. Area between pale bands irregularly patterned but with distinctly paler center and dark brown edges (Fig. 118). Venter cream with little scattered pigmentation. Juvenile paratype (TM 85002) similar to adult paratype but with anterior pale trunk band asymmetricalexpanded on right side and containing a single dark blotch (Fig. 118).

Distribution.- The species is known only from Farm Uithoek in the Tsumeb District of northeastern Namibia (Figs. 10-11). This is one of the most isolated members of the Pachydactylus weberi group, occurring 125 km north-northeast of $P$. waterbergensis and almost 400 km westsouthwest of $P$. tsodiloensis. The locality lies near the northern point of a relatively low range of hills that extends northward from the main body of the Otaviberge. It seems likely that the species is more widely distributed within the Otaviberge. Uithoek is very close to the farm Ghaub, where an isolated population of Rhoptropus barnardi has been reported (W.D. Haacke, pers. comm., 2004). The region as a whole has been poorly explored herpetologically, and may be expected to harbor other isolated populations and/or endemic species of lizards. A number of endemic invertebrates and fish are already known from the Otavi-Tsumeb-Grootfontein area (Barnard et al. 1998).

Natural History.- The area where P. otaviensis occurs may be characterized as mountain savanna and karstveld (Giess 1971). The paratypes were collected in broadleaf savanna on rocky dolerite mountains. Like most members of the P. weberi complex, P. otaviensis probably shelters in rock cracks. An undescribed congner (see below) co-occurs with this form in the Otavi Highlands.

Conservation Status.- Pachydactytlus otaviensis does not occur in any protected areas. Depending upon the extent of its actual range it may be under some threat from local mining activity.

Remarks.- The type locality of Pachydactylus otaviensis was plotted by Visser (1984) in his range map of $P$. weberi. Bauer and Lamb (2003) also mentioned the holotype and suggested that it
might represent a close relative of $P$. tsodiloensis and/or $P$. waterbergensis, perhaps separated as the result of movements of the Kalahari sands.

## Undescribed species in the Pachydactylus serval/weberi group

In addition to the species recognized and described above, we have identified at two additional distinctive members of the Pachydactylus serval/weberi complex. These are presently known from only a few specimens and will be described elsewhere when additional material becomes available.

## Pachydactylus sp. 1

Material Examined.- South Africa: Northern Cape Province: TM 84939, Aughrabies Falls National Park ( 2820 Cb ); TM 85286, Farm Zeekoe, Steek 9, Kenhardt district ( $28^{\circ} 29^{\prime} 17^{\prime \prime} \mathrm{S}, 20^{\circ} 07^{\prime} 34^{\prime \prime} \mathrm{E}$ ); ZFMK 83354, Augrabies National Park. Namibia: Karasburg District: NMNW R 10494; Haib Mine ( $28^{\circ} 41^{\prime} 49^{\prime \prime} \mathrm{S}, 17^{\circ} 53^{\prime} 26^{\prime \prime} \mathrm{E}$ ).

Remarks.- The first species is superficially most similar to $P$. mclachlani and $P$. robertsi and is known from two widely separated localities along the Orange River - Haib Mine in the west, where it is sympatric with $P$. mclachlani, and Augrabies in the east, where it occurs in large granitic slabs and is the only member of the $P$. weberi complex that is present.

## Pachydactylus sp. 2

Material Examined.- Namibia: Grootfontein District: TM 84999. 85005, Farm Uisib, 15 km NW (straight line) Otavi ( $19^{\circ} 33^{\prime} 08^{\prime \prime} \mathrm{S}, 17^{\circ} 14^{\prime} 07^{\prime \prime} \mathrm{E}$ ).

Remarks.- A second species, at present known from only a hatchling and a juvenile, has the tubercular dorsum and thighs typical of the $P$. weberi complex, but the rostral scale narrowly contacts the nostril rim, as is typical for the members of the $P$. serval complex. The juvenile pattern expressed by this species is unique and diagnostic. This species has been collected in thick woodland in dolerite mountains in the Otaviberge, in close proximity to $P$. otaviensis.

## Incertae sedis

A number of specimens examined could not be unambiguously assigned to species. Some of these were either $P$. serval or $P$. montanus. which can share nearly identical adult patterns and occur in sympatry in parts of southern Namibia. Localitiies associated with these specimens, however, are of minor interest as they occur well within the confirmed ranges of the two species. However, several specimens in the $P$. weberi group proved to be problematic and will be discussed elsewhere. All have relatively large body scales and some evidence of a nape band. but no other body banding. These specimens are SAM 47075 (Ugab River at $20^{\circ} 52^{\prime} \mathrm{S}, 14^{\circ} 57^{\prime} \mathrm{E}$ ), TM 52503 (Leerkrans Farm, Northern Cape Province, South Africa, 2821 Bc ) and PEM R 12857-60 (Aus, Lüderitz District, Namibia, 2616 Cb ). The first specimen is most similar to $P$. reconditus. Although its locality is precise, additional material from this area is necessary to confirm that geckos from this locality are conspecific with those from the Khomas Hochland. The specimen from the Leerkrans locality is superficially similar to both $P$. robertsi and the undescribed species from Augrabies (Pachydactylus species 1). Those from the last locality may assignable to $P$. acuminatus, but this also requires further inquiry. The Leerkrans record is significant as it represents the easternmost record of any member of the $P$. weberi group. A single specimen in the $P$. serval complex (TM 84999) is particularly perplexing. It is superficially identical to typical $P$. montanus, but was collected hundreds of kilometers away, indeed hundreds of kilometers north of the northernmost record of any member of the
P. serval complex in the Khumib River bed, approximately 30 km northwest of Puros ( $18^{\circ} 39^{\prime} 17^{\prime \prime} \mathrm{S}$, $12^{\circ} 39^{\prime} 27^{\prime \prime} \mathrm{E}$ ).

## Excluded from the Pachydactylus serval group

## Pachydactylus sansteynae Steyn and Mitchell, 1967

Figures 119-121.
1967 Pachydactylus serval sansteyni Steyn and Mitchell, Cimbebasia (21):11, figs. 1-2 (Holotype: NMNW R 1626 (formerly CR 4478/4): "the vicinity of Kuidas water-hole in the Southern Kaokoveld, (about $13^{\circ} 45^{\prime}$ E., $20^{\circ} 38^{\prime}$ S., altitutde about $1200^{\prime}$ )," coll. C. Brits, 3 April 1966. Paratypes: CR 4478/3: same locality as holotype, coll. P. Motonane, 3 April 1966; CR 4478/1-2, 4478/5-7: same locality as holotype, coll. W. Steyn, A. Visagie, P. Motonane, 3 April 1966; CR 3057: "ten miles inland from the Huab river mouth," coll. F. Brown, 28 June 1966; CR 2838: " 5 miles north of the Huab river mouth, near the coast," coll. P. Motonane, 24 April 1966. See Remarks).

1971 Pachydactylus serval sansteyni Mertens, Abhandl. Senckenberg. naturf. Ges. 529:43.
1982 Pachydactylus serval sansteyni Welch, Herpetology of Africa:36.
1988 Pachydactylus sansteyni Branch, Field Guide:207.
1991 [Pachydactylus] sansteyni Kluge, Smithson. Herpetol. Inform. Serv. 85:23.
1993 [Pachydactylus] sansteyni Kluge, Gekkonoid Lizard Taxonomy:25.
1993 Pachydactylus sansteyni Bauer et al. Madoqua 18:127.
1994 Pachydactylus sansteyni Welch, Lizards of the World 1:95.
1994 Pachydactylus sansteyni Branch, Field Guide, 2nd ed.:207.
1998 Pachydactylus sansteyni Branch, Field Guide, 3rd ed.:261.
2000 [Pachydactylus] sansteyni Rösler, Gekkota 2:99.
2001 [Pachydactylus] sansteyni Kluge, Hamadryad 26:21.
2002 Pachydactylus sansteyni Bauer et al., Proc. California Acad. Sci. 53:23.
2003 Pachydactylus sansteyni Griffin, Namibian Reptiles:38.
2004 Pachydactylus sansteynae Michels and Bauer, Bonn. Zool. Beitr. 52:87.
2005 P[achydactylus]. sansteynae Bauer and Lamb, Afr. J. Herpetol. 54:116.
Material examined.- Namibia, Swakopmund District: TM 31374, 56 km N Cape Cross (2113Bc); TM 44171, Cape Cross (2113Dd); TM 24983-84, 63377-78, Messum Mts. (2114Ac); Khorixas District: CAS 214589*, Skeleton Coast National Park, ca. 1 km S of Huab River Bridge ( $20^{\circ} 54^{\prime} 03^{\prime \prime} \mathrm{S}$, $13^{\circ} 32^{\prime} 01^{\prime \prime} \mathrm{E}$ ); CAS 214767*, Skeleton Coast National Park, N bank of Huab River at Huab River Bridge ( $20^{\circ} 54^{\prime} 04^{\prime \prime} \mathrm{S}, 13^{\circ} 31^{\prime} 30^{\prime \prime} \mathrm{E}$ ); NMNW R 1622, 5 miles north of the Huab River mouth, near the coast ( 2013 Cc ); NMNW R 1623-5, 1637 (paratypes), 1626 (holotype), Kuidas (2013Da); TM 56997, 35 km SE Torra Bay, Skeleton Coast National Park ( $20^{\circ} 35^{\prime}$ S, $13^{\circ} 21^{\prime} \mathrm{E}$ ); NMNW R 7690, 20 mi . N of Ugab River mouth on Coast (2013Cd); TM 32019, $\pm 20 \mathrm{mi}$ N Ugab River mouth (2013Cd); TM 62988, Uniab River 6 km E dunefield ( $20^{\circ} 08^{\prime} \mathrm{S}, 13^{\circ} 19^{\prime} \mathrm{E}$ ); Opuwo District: NMNW R 140, TM 57700, Möwe Bay ( $19^{\circ} 22^{\prime} \mathrm{S}$, $12^{\circ} 41^{\prime} \mathrm{E}$ ); TM 56998 , 4 km NE Möwe Bay ( $19^{\circ} 20^{\prime} \mathrm{S}, 12^{\circ} 45^{\prime} \mathrm{E}$ ); TM 57053, Sarusas ( $18^{\circ} 45^{\prime} \mathrm{S}, 12^{\circ} 23^{\prime} \mathrm{E}$ ); TM 32849, Khumib River 13 km E dunefield, Skeleton Coast National Park (1812Dc); TM 63377-78, Cape Fria Hut ( $18^{\circ} 15^{\prime} \mathrm{S}, 12^{\circ} 01^{\prime} \mathrm{E}$ ); TM 32503, NW Dunefields (1711Da).

Diagnosis.- To 48.0 mm SVL (TM 63377). Pachydactylus sansteynae is not a member of the P. serval/weberi group, but is listed here because it was initially described as a subspecies of $P$. serval (Steyn and Mitchell 1967). Dorsal pattern usually consisting of dark vermiculations, but may be spotted (e.g., TM 24983, 32849, 56998). Juvenile pattern as adult. It may be distinguished from $P$. serval, P. purcelli, P. montanus, P. kobosensis, P. carinatus, and P. griffini by the presence of conical tubercles on the hind limbs and from all other members of the $P$. serval/weberi group by its ros-tral-nostril contact. In addition, $P$. sansteynae is characterized by an elongate head, a lack of tubercles on the interorbital and parietal regions, 14-16 rows of very small, keeled tubercles (usually evident only posterior of the axillae), typically 4 undivided lamellae beneath digit IV of the pes, and
greatly enlarged cloacal spurs in males, consisting of four enlarged, pointed, sharp-edged scales (Figs. 119-121).

Distribution.- Griffin (2003) reported the species from the Opuwo, Khorixas, Omaruru and Swakopmund districts in northern Namibia. Within this area it is limited largely to areas within 20 km of the coast, bounded by the Kunene River in the north and the Omaruru River in the south (Figs. 10-11). Given its occurrence in the far north of the Skeleton Coast, it is highly likely that $P$. sansteynae also occurs in southwestern Angola, although no specimens have been collected there to the best of our knowledge.

Natural History.- We have collected this species only near the Huab River mouth, where it was found sheltering in crevices in highly fragmented shale slopes (Fig. 122). It is uncommon for Pachydactlyus to occur in circumstances in which soil or mud is present in rock crevices, but this was the case for this species. Steyn and Mitchell (1967) reported that the types were associated with boulders or sandstone blocks and that they were found walking on the sand at night.

Conservation Status. - The species is certainly secure. Its entire range is in the uninhabited, hyperarid northern Namib and nearly all localities lie within the Skeleton Coast National Park or West Coast Recreation Area.

Remarks.- The description gives data for the holotype and eight paratypes, as well as three other specimens. Material in the National Museum of Windhoek bearing "CR" numbers have since been catalogued into the main collection. The holotype is present as NMNW R 1626 and there are four specimens labeled as paratypes, NMNW R 1623-5 and NMNW R 1637. The whereabouts of the other paratypes and three additional specimens could not be determined. There are no specimens in the Windhoek collection, or in the Transvaal Museum (where CR 2838/1, a non-type, was supposedly sent) that correspond to the missing material. However. NMNW R 1622, labeled as a paratype with the data "14 mi. N Swakopmund" collected 29 September 1965 by P. Motonane is likely, in reality, to correspond to CR 3871//2, a non-type, that was, according to Steyn and Mitchell (1967), collected on this date, by this collector. but from " 5 miles north of the Huab river mouth, near the coast." The confusion of localities is probably associated with the switch from "CR" to SMW (and subsequently NMNW) numbers and labels when the original data were probably inadvertently exchanged between specimens. The locality near Swakopmund is outside of the range of this species and no appropriate habitat for this species occurs there, but the superficially similar $P$. bicolor is common at this place. A purported photograph of P. sansteynae (Branch 1998, pl. 112, upper left) actually illustrates a specimen of this northcentral Namibian coastal population of $P$. bicolor.

This species was named for "Mrs. STEYN, in acknowledgement of her collecting and voluntary curatorial activities on behalf of the State Museum" (Steyn and Mitchell 1967:11). Article 31.1.2 of the International Code of Zoological Nomenclature (1999) states that "A species-group name, if a noun in the genitive case ... formed directly from a modern personal name, is to be formed by adding to the stem of that name $-i$ if the personal name is that of a man, -orum if of men or of man (men) and woman (women) together, -ae if of a woman, and -arum if of women; the stem of such a name is determined by the action of the original author when forming the genitive." The original construction, sansteyni, was thus incorrectly formed. Following Article 33.3.3 of the Code, Michels and Bauer (2004) emended the name to Pachydactylus sanstevnae. The need to correct the name probably escaped earlier notice because the species is restricted in range and seldom cited in the literature, the journal in which the description is held is not widely known outside of southern Africa, and the etymology of the name appears in the general introduction to the paper, rather than within the species description proper.

Steyn and Mitchell (1967) regarded this gecko as a subspecies of $P$. serval, with which it shares
a generally similar habitus and spotted dorsum. It was regarded as specifically distinct by Branch (1988) and all subsequent authors. A broader phylogenetic analysis reveals that it is only distantly related to the P. serval/weberi group. Its closest affinities lie with a number of small-bodied Pachydactylus that share a chiefly northwestern Namibian distribution (Bauer and Lamb 2005; Lamb and Bauer 2006).

## Valid species of the $P$. serval/weberi complex

P. fasciatus Boulenger, 1888
P. weberi Roux. 1907
P. serval Werner, 1910
P. purcelli Boulenger, 1910
P. montanus Methuen \& Hewitt, 1914
P. werneri Hewitt, 1935
P. kobosensis FitzSimons, 1938
P. robertsi, FitzSimons, 1938
P. acuminatus FitzSimons, 1941
P. tsodiloensis Haacke, 1966
P. waterbergensis Bauer \& Lamb, 2003
P. reconditus sp. nov. Bauer, Lamb \& Branch, 2005
P. monicae sp. nov. Bauer, Lamb \& Branch, 2005
P. griffini sp. nov. Bauer, Lamb \& Branch, 2005
P. carinatus sp. nov. Bauer, Lamb \& Branch, 2005
P. mclachlani sp. nov. Bauer, Lamb \& Branch, 2005
P. visseri sp. nov. Bauer, Lamb \& Branch, 2005
P. goodi sp. nov. Bauer, Lamb \& Branch, 2005
P. otaviensis sp. nov. Bauer, Lamb \& Branch, 2005

## Comparisons among taxa

One of the most distinctive members of the Pachydactylus serval/weberi group is $P$. kobosensis, which may be distinguished by the exclusion of both the rostral and first supralabial scales from the nostril rim, the increased number of subdigital lamellae ( 6 vs 5 undivided lamellae beneath digit IV of pes), and its velvety dorsal skin.

Within the Pachydactylus serval/weberi complex, the "serval type" species (P. serval, P. purcelli, P. montanus, P. griffini, P. carinatus) may be distinguished from all remaining forms by the condition of rostral-nostril contact and the absence of thigh tubercles. Among these forms $P$. serval and $P$. carninatus share a juvenile pattern characterized by a dark body with pale sacral and nape markings, whereas $P$. purcelli and $P$. montanus have banded juveniles ( 3 bands in the former, 4 in the latter), and $P$. griffini juveniles are spotted. Adults of $P$. purcelli and $P$. montanus often retain recognizable elements of the juvenile pattern, and adult spotting in the former is characteristically close-spaced and covers the whole of the dorsum and flanks. Further, original tails of $P$. serval and $P$. purcelli bear small, unkeeled tubercles, whereas these are typically keeled in $P$. griffini and $P$. carinatus and usually so in $P$. montanus. Only in $P$. carinatus is the dorsum always covered by keeled tubercles. In contrast, keeled tubercles (if present) in $P$. montanus are generally lacking form the mid-dorsum and there are maximally 12 (vs. 16) tubercular rows. Although juvenile (and usually smaller adult) specimens of all members of the group may be easily distinguished on the basis of color pattern, large adult specimens of $P$. montanus and $P$. serval may be difficult to distinguish, although in the former there is a greater difference in relative size between snout and interorbital scales and small parietal tubercles are often present.

All remaining members of the group possess the "weberi type" condition, in which the rostral (but usually not the first supralabial) is excluded from the nostril, and the thighs bear enlarged, usu-ally-keeled or conical, tubercular scales. Within this group P. visseri, P. tsodiloensis, and P. waterbergensis possess five or more transverse body bands and juvenile patterns, when known, are essentially similar to the adult. Of these, $P$. visseri typically has 6-7 pale bands that are wider than the darker interspaces. Pachydactylus tsodiloensis and $P$. waterbergensis are most similar to one another, but the former has generally thicker and more irregular light body bands and is larger (maximum 60 vs 49 mm SVL) and has morer subdigital lamellae ( 6 vs 5 undivided beneath digit IV of pes).

Both P. robertsi and $P$. reconditus have a distinctive light nape band, but lack bands on the remainder of the trunk. These forms may be distinguished from one another by their dorsal tubercles, which are large, rounded and partly imbricating in the former and somewhat smaller, more elongate and juxtaposed in the latter. Pachydactylus werneri is distinguished by its elongate body and limbs, raised nostril rims and a juvenile pattern of four pale transverse bands (often highly modified in adults). All remaining species have three pale transverse bands as juveniles. Pachydactylus fasciatus is the most strongly tuberculate of these, has very wide bands, and is the only species in which caudal tubercles are typically in contact with each other, without intervening scales. In $P$. mclachlani there are two narrow bands - on the nape and anterior of midbody. In juveniles and most adults a broader pale band crosses the sacrum, but this fades and may be inconspicuous in some adults, giving the impression that only two bands are present. Pachydactylus acuminatus may be distinguished from the remaining taxa by its greater number of undivided subdigital lamellae (6 vs 5 beneath digit IV of pes) and by its highly heterogeneous tuberculation (typically much reduced on anterior third of trunk). In P. otaviensis, the three dorsal bands may be distinct or the centers of the interspaces between bands may be similar in color to the bands themselves, yielding a pattern of 5-6 narrow dark bands (the borders of the pale bands) on a light background. The dorsal, thigh and caudal tubercles are strongly keeled to mucronate and the cloacal spurs are especially welldeveloped. Pachydactylus weberi, P. monicae, and $P$. goodi all share the three-banded juvenile pattern, but this is typically greatly obscured in $P$. weberi adults, which usually possess a complex dorsal pattern. In the other two species, the three-banded pattern remains evident in the adults, being weakly contrasting and usually flecked with dark markings in $P$. monicae and boldly contrasting against a dark brown background in $P$. goodi.

## Key to the Members of the Pachydactylus serval and P. weberi Groups

Unambiguous identification of some species, particularly in the $P$. sen al complex, requires hatchling or juvenile specimens, which are distinctive with respect to dorsal patterning. However, subtle differences in adult pattern and scalation, as well as geographic information should permit the identification of adults in most instances.

[^9]$\ddagger \mathrm{b}$. Dorsal scalation strongly tuberculate, tubercles keeled, usually with whitish tips, conical tubercles on parietal table
P. carninatus
5a. Juveniles with three cross bands, adults with small, irregular, dense spots (southern populations) or retaining evidence of juvenile pattern (northern populations) adults usually without body tubercles
P. purcelli

5 b. Juveniles with four cross bands, adults with relatively large spots and/or evidence of cross bands, adults with variably developed body tuberculation in 10-12 rows
P. montanus

6a. Rostral and first supralabial excluded from nostril, dorsal scalation largely homogeneous
P. kobosensis

6b. Rostral only excluded from nostril . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7
7a. Nape band only or no body bands . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8
7b. Two or more body bands present . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9
8a. Dorsal tubercles rounded, partly imbricating . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . P. robertsi
8b. Dorsal tubercles oval, juxtaposed . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . reconditus
9a. Five or more body bands. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10
9b. Three or four body bands . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 12
10a. Large, to 60 mm SVL, typically 6 undivided lamellae beneath digit IV of pes. . P. tsodiloensis
10b. Body size small to moderate ( $35-53 \mathrm{~mm}$ SVL), typically 5 undivided lamellae beneath digit IV of pes.
11a. 16-18 rows of dorsal tubercles, 6-7 pale dorsal markings, wider than dark cross bands
P. visseri

11b. 20 rows of dorsal tubercles, 5-6 narrow pale bands on reddish-brown background
P. waterbergensis

12a. Body gracile, limbs long, slender, nostril rims inflated, 4 pale transverse bands (pattern often obscured in adults). . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . P. werneri
12b. Body and limbs relatively robust, nostril rims not inflated, 3 pale transverse bands in juveniles (may be obscured in adults) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 13
13a. Body large (to 56 mm SVL), transverse bands wide, bold and strongly contrasting with background color in both juveniles and adults, caudal tubercles within a single tail whorl abutting P. fasciatus

13b. Body moderate (to 50 mm SVL), transverse bands distinct in juveniles, variable in adults, caudal tubercles within a single whorl not in contact. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14
14a. Anterior third of dorsum weakly tuberculate, typically 6 lamellae beneath digit IV of pes, all dorsal bands relatively broad. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . P. acuminatus
14b. Entire dorsum approximately equally tuberculate, 5 or 6 lamellae beneath digit IV of pes . 15
15a. Dorsal scales very large, strongly keeled to mucronate, dorsum pale with six dark cross bands
P. otaviensis

15b. Dorsal scales moderate, keeled but not mucronate. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 16
16a. Transverse bands all broad . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 17
16b. Anterior transverse bands narrow, sacral band may be inconspicuous in adults . P. mclachlani
17a. Background color of adult dorsum dark brown. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . P. goodi
17b. Background color of adult dorsum light (cream to light brown) . . . . . . . . . . . . . . . . . . . . 18
18a. Dorsal bands, except that on nape generally obscured in adults, dark margins of pale bands with slightly wavy margins, usually with extensive dark patterning on dorsum . . . . P. weberi
18b. Dorsal bands generally retained in adult, dark margins of pale bands with straight edges, dark patterning limited to edges of cross bands and scattered dashes or blotches within and between bands
P. monicae

## DISCUSSION

Molecular Comparisons.- Intraspecific pairwise comparisons of cytb sequence divergence, derived from Kimura's (1980) 2-parameter model, ranged from 0.0 to $18.5 \%$. The greatest distances were observed in P. montanus, reflecting marked divergence between geckos collected south of the Orange River near Onseepkans and the remaining populations north through the Karasberg area (range $=14.3-18.5 \%$ ). Genetic divergence within the other species surveyed was significantly lower, ranging from 0.5 to $10.7 \%$. Interspecific comparisons of sequence divergence, both within and between respective weberi and serval groups, fall in the middle to higher end of values reported for cytb in reptile (and other vertebrate) congeners (Johns and Avise 1998). All interspecific comparisons exceed $12 \%$, and some comparisons approach $30 \%$. As might be expected, these high levels of divergence are reflected in near saturation of third position codon sites (substitutions for 124 out of 128). Thus, the serval/weberi clade exhibits sequence divergence comparable to that of other Pachydactylus clades, including small-bodied groups, e.g., the capensis (Bauer and Lamb 2002) and rugosus groups (Lamb and Bauer 2000), and large-bodied groups, e.g., the namaquensis group (Lamb and Bauer 2002). A higher order molecular phylogeny of Pachydactylus as a whole (Bauer and Lamb 2005; Lamb and Bauer 2006) reveals that the weberi/serval clade is sister taxon to the capensis clade.

Phylogenetic Relationships in the Pachydactylus serval Group.- Relationships among members of the Pachydactylus serval and weberi groups remain incompletely known as we were only able to obtain genetic samples from 15 of the 21 species we recognize within the group. Further, as noted earlier, our genetic data consist of a segment of a single mitochondrial gene (cytb); thus, it is quite possible that the gene tree may differ topologically from species trees derived from sampling a larger set of independent characters

The Bayesian analysis (Fig. 123) retrieves a monophyletic weberi clade corresponding to that recognized on the basis of morphological characters (rostral excluded from nostril and thighs tuberculate, except $P$. kobosensis). Within this group, P. fasciatus, $P$. waterbergensis and P. tsodiloensis form a well supported subclade $(\mathrm{pP}=0.99)$ that is sister to the subclade $P$. weberi sensu stricto $(\mathrm{pP}$ $=0.92$ ). Together, these two subclades constitute the sister group to all remaining members of the weberi complex. which form a well supported assemblage ( $\mathrm{pP}=1.0$ ) with the following relationships: ((((P. wemeri, P. reconditus)P. kobosensis) (P. robertsi, P. "Augrabies")) P. monicae). Support for the entire weberi group, however, is weak ( $\mathrm{pP}=0.75$ ). Unfortunately genetic material was not available for $P$. acuminatus, P. visseri, P. goodi, or P. mclachlani, but all exhibit morphological features consistent with the $P$. weberi group and we hypothesize that they are also members of this clade.

The $P$. serval group is retrieved but not strongly supported in the Bayesian analysis (posterior probability $<0.80$ ). Within this group the clade ( $(P$. serval. P. griffini) $P$. carinatus) is retrieved with strong support. although the clustering of $P$. serval and $P$. griffini is weak. The remaining serval group members. P. montanus and P. purcelli, are each other's sister taxon and constitute the sister group of the remaining species of the serval complex. Sampling within $P$. montanus was more extensive than in any other group and this taxon shows greater genetic variability than any other taxa sampled. In particular, specimens from the immediate vicinity of Onseepkans differed considerably from those elsewhere in the species range, including localities as little as 55 airline km away. Specimens from Kakamas and Augrabies (south and east of Onseepkans) are much closer to those from the Grünau region (north and west of Onseepkans) than either are to animals from the immediate vicinity of Onseepkans. Further. specimens from Farm Witputs, on the north bank of the Orange River, fell into two different subclades of $P$. montanus (Fig. 124).


Figure 123. Bayesian gene tree of the Pachydactylus serval/weberi clade based on sequence data from a portion of the cytochrome $b$ gene. Bold lines indicate posterior probabilities $(\mathrm{pP})>0.90$. Unlabeled lines indicate $\mathrm{pP}<0.80$. Branches with $0.80<\mathrm{pP}<0.90$ indicated explicitly. Numbers refer to museum numbers. Unless otherwise indicated, specimens are in the collection of the California Academy of Sciences (CAS). See text for standard museum symbolic codes. See Appendix for GenBank accession numbers corresponding to these specimens. Additional specimens investigated, but with identical sequences to those shown here, are not indicated.


Figure 124. Detail of Bayesian gene tree of Pachydactylus montanus based on sequence data from a portion of the cytochrome $b$ gene. Subclades are color-coded and localities are numbered to correspond to points plotted on the satellite image of the Orange River and adjacent areas of South Africa and Namibia. There is generally good fit between apparent relationships and geographic patterns, but specimens from Onseepkans are highly divergent from their nearest neighbors, despite exhibiting no obvious morphological differences. See text for further discussion. MODIS imagery from the Global Land Cover Facility (http://www.landcover.org).

Our results suggest congruence between mtDNA tree-based and morphological characterbased methods for delimiting species boundaries in both the serval and weberi groups. The species identified in this study are all also geographically concordant, with ranges that are contiguous intraspecifically but largely allopatric or parapatric between taxa. The major exception to our concordant tree- and character-based delimitations is in respect to $P$. montanus. In this instance cytb data suggest that the Onseepkans population forms a deeply divergent basal lineage within $P$. montanus. However, the genetic distinctiveness of the Onseepkans population is not corroborated by any morphological characters and appears to be at odds with distributional data as well. For these reasons, we have elected to treat all of these populations as members of a single species, but should additional molecular and/or morphological data substantiate the distinctiveness of the Onseepkans population, the name $P$. onscepensis remains available for it.

Our taxonomic conclusions differ substantially from those of earlier workers, reflecting in large part our extensive sampling effort ( $>1800$ specimens) throughout the range of the Pachydactylus serval and weberi groups. This includes material that we and our colleagues collected in the Richtersveld and adjacent southern Namibia and in the Karasberg region. These areas, which include several regional endemics, were poorly collected prior to the mid-1970s. In addition, our revision reflects the use of previously under-utilized characters, particularly juvenile coloration pattern, as well as the mtDNA data.

McLachlan and Spence's (1966) interpretation of the serval group represents the most recent explicit consideration of relationships and taxonomic boundaries in this species complex. They recognized a single species with three subspecies. P. s. serval, P. s. purcelli, and P. s. onscepensis. Their subspecific designations were based chiefly on perceived patterns in dorsal tuberculation, with purcelli possessing no tubercles, serval having few tubercles and onscepensis being moderately to strongly tuberculate. We agree that $P$. purcelli is virtually completely atuberculate throughout its range. Based on our conclusions, however. McLachlan and Spence (1966) misinterpreted their data on tuberculation from specimens along the length of the lower Orange River. They regarded the degree of tuberculation to be largely clinal in nature, with populations from Onseepkans downstream exhibiting greater tuberculation and being referable to $P$. s. onscepensis. Our data support the interpretation that the Richtersveld ( 175 airline km and more downstream from Onseepkans) is occupied by a strongly tuberculate species ( $P$. carinatus). whereas $P$. montanus, which exhibits high variability with respect to tuberculation. occurs chiefly upstream from Goodhouse. The two species
appear to occur sympatrically, or nearly, so in several areas along the Orange River from Vioolsdrif to Onseepkans. McLachlan and Spence (1966) likewise regarded low to moderate tuberculation in the area near the Great Karas Mountains as reflecting the exclusive presence of P. s. serval in this region. Our data, however, indicate that three species, $P$. serval, $P$. montanus and $P$. purcelli, occur in the Karasberg area: $P$. serval, as currently defined, probably reaches the limits of its distribution in this region.

## Biogeography and the Evolutionary History of the Pachydactylus serval Group

Ecological Correlates of Distribution.- With the exception of several problematic outliers, geographic patterns within the Pachydactylus serval and weberi complexes are coherent. The clade as a whole occupies much of western southern Africa exclusive of coastal areas, most of the Kalahari and the southwestern Cape. However, existing collections provide an incomplete picture of the geographic distribution of individual species. The distributional limits of even well-known forms represented by hundreds of specimens remain incompletely determined, and large areas of both Namibia and South Africa that may support members of this group remain to be surveyed adequately. In particular, the region between Keetmanshoop and Rehoboth in south central Namibia and Boesmanland in the Northern Cape have been undercollected.

Specific correlates of distribution with vegetation patterns (Giess 1971; Mucina and Rutherford 2004) are tenuous at best. However, the P. serval clade appears to be restricted largely to the NamaKaroo Biome, with the Richtersveld and adjacent populations also occupying the Succulent Karoo and Desert biomes, although in the last case, populations are chiefly associated with the riparian Orange corridor (Jürgens 1991; Irish 1994). Interestingly, a single P. montanus- like animal was collected from the Kaokoveld, in the narrow corridor of the Nama-Karoo Biome that extends northwards to the Kunene River. Members of the $P$. weberi group are more broadly distributed across biomes, with several Savanna Biome species ( $P$. tsodiloensis, P. otaviensis, $P$. waterbergensis, $P$. recoditus and $P$. kobosensis), a Desert Biome species ( $P$. werneri), three Nama-Karoo Biome species ( $P$. robertsi, P. goodi and $P$. mclachlani), a succulent Karoo species ( $P$. weberi), and several others with distributions spanning biomes. This is especially true in the Richtersveld and adjacent southern Namibia, where many vegetation types and phytogeographic units meet in a relatively small area (Jürgens 1991; Mucina and Rutherford 2004).

Endemism.- The recognition of many resurrected and new taxa here provides the context for reassessing endemism within this group, which previously consisted chiefly of just a few widespread taxa (Branch 1998). Our revision reinforces views of Namibia as a country characterized by high biodiversity and endemism (Maggs et al. 1998). M. Griffin (1998) identified 55 reptile species as being strictly or primarily endemic to Namibia and emphasized the significance of the inselbergs of western Namibia as centers of endemism. This revision, together with other recent species descriptions (Bauer et al. 2002; Bauer and Lamb 2003a), underscores the contribution of Pachydactylus to overall endemism. In particular, two clades, the northwestern clade (sensu Bauer and Lamb 2005) and the serval/weberi clade, account for the majority of Namibian endemics. The latter clade is notably absent from northwestern Namibia along the Northern Namibian Escarpment (sensu Irish 2002), an area where the northwestern clade (sensu Bauer and Lamb 2005) has its greatest species richness. This region is also largely coincident with the Kaokoveld center of Floral Endemism (Volk 1966; van Wyk \& Smith 2001) and is recognized as a regional center of endemism for reptiles in general (Crowe 1990; Simmons et al. 1998; Griffin 2000b).

Within the servallweberi clade, areas of endemism include montane regions that have been
ranked as areas of high biodiversity importance (Irish 2002), e.g., the Karasberge, the Otavi Highlands, and the Waterberg. Although biotic diversity of the Waterberg is high, endemism is generally low (Simmons et al. 1998). The Waterberg's relatively low relief probably facilitates movement of terrestrial reptiles from surrounding areas, decreasing the likelihood of long-term isolation (and thus endemism), while promoting diversity through the commingling of western (Namib and central Namibian) and eastern (Kalahari) faunal components. As a result, the herpetofauna of the Waterberg Plateau region is diverse, with 13 frogs and a minimum of 82 reptile species (Schneider 1998; van den Elzen 1978), of which only the lacertid Pedioplanis rubens (Mertens, 1954) - one of only two rock-dwelling members of its genus (Mayer and Richter 1990) - and Pachydactylus waterbergensis are endemic. In both instances speciation was probably more a function of high substrate specificity (sandstone cliffs and boulders) than the result of isolation by distance or elevation.

Bauer (1999) emphasized substrate specificity as an important factor in the promotion of cladogenesis in the Pachydactylus Group as a whole. The historical interplay of sand and rock substrates has resulted in the isolation and subsequent speciation of obligate rupicolous species on inselbergs isolated by sandy substrates (Haacke 1982; Bauer 1993). For example, Bauer (1999) considered shifts in the Namib sand seas as causative in the diversification of Rhoptropus, whereas changes in the extent of the Kalahari sands (Thomas and Shaw 1993) have implicated in speciation of strictly rupicolous Platysaurus (Broadley 1978; Jacobsen 1994; Scott et al. 2003). Changing patterns of substrate distribution may be the result of orogenic events, such as the uplift of the great Western Escarpment about 18 MY (Moon and Dardis 1988; Partridge and Maud 2000), or of climatic shifts, such as cooling associated with the development of the south polar ice cap (Woodruff et al. 1981) and the initiation of the cold Benguela current system along the west coast in the Late Miocene (Siesser 1978, 1980; Coetzee 1993) or cooling and drying caused by the northward rift of the African continent and the closure of the Tethys seaway (Axelrod and Raven 1978; Tyson 1986; Tyson and Partridge 2000).

Within the Pachydactlyus serval/weberi clade, P. tsodiloensis is restricted to the remote Tsodilo Hills of northwestern Namibia. Like the Waterberg, these hills are not very high (to 330 m above the surrounding plains), but they provide the only extensive rocky habitat for rupicolus geckos for great distances in any direction. The same is true of the Otavi Highlands, from which we have identified two endemic Pachydactylus - P. otaviensis and an as yet undescribed species. Other northern Namibian inselbergs, such as the Aha Mountains, have not yielded $P$. weberi type geckos (Haacke 1966), but have not been adequately sampled. Most of the areas of endemism occupied by members of this group are also identified by other taxa; for example, the bothriurid scorpion Lisposoma joseehermanorum is restricted to the Otavi Highlands (Prendini 2003a).

Similar substrate mediated cladogenesis may have played a role elsewhere in the range of the serval and weberi groups. For example, the granitic Aus mountains are separated from the dolomitic Huib-Hoch Plateau in southern Namibia by a sandy corridor as little as 10 km wide. Nonetheless, this corridor appears to be a barrier between $P$. acuminatus in the north and $P$. monicae and $P$. visseri in the south. A similar barrier has been noted for scorpions, which are likewise substrate specific (Prendini 2001b, 2003b). In other cases. multiple montane units with contiguous corridors of suitable rocky substrate may support more widespread species. For example, $P$. reconditus occurs in the Swakop-Khan, Khomas Hochland, Auas. Gamsberg and other montane areas identified by Irish (2002).

The most significant areas of endemism and diversity for the $P$. serval/weberi clade are in the Karasberge and along the Orange River downstream from Augrabies Falls. Lawrence (1929) first regarded southeastern Namibia. including the Karas Mountains, as a recognizable area of reptile endemism, but until now this has been supported by few taxa. To the west, Bauer and Branch (2003)
and Scott et al. (2003) emphasized the high level of lizard endemism in the Richtersveld and immediately adjacent areas. They noted the role the Orange River plays as a barrier to gene flow for a few species, but also its more important role as a corridor for dispersal.

Bauer (1999) specifically suggested a role for the Orange River in the history of the Pachydactylus serval group, and the distribution of many of its constituent taxa ( $P$. carinatus, $P$. montanus, $P$. goodi, $P$. monicae, $P$. visseri, $P$. weberi) along the river or with the river as an apparent barrier to dispersal, certainly suggests that this is the case. However, specific scenarios relating the changing position of the Orange drainage since the Cretaceous to the patterns observed today are not straight-forward. One purely speculative hypothesis is that the Oligocene position of the Orange far to the south of its present position, with its mouth at the Cape Canyon, near the modern Olifants River mouth (Dingle and Hendy 1984; Dollar 1998; Goudie 2005), may have allowed the expansion of a chiefly northern lineage well into South Africa. Subsequent capture of the Orange by the Koa River in the Late Miocene may have isolated one lineage in Namaqualand, whereas later establishment of the modern drainage pattern, following the failure of the Koa through tectonic agency or aridification (Dollar 1998; De Wit 1999), may have isolated another lineage east of Namaqualand and south of the modern course of the Orange. The proposed extensive Kalahari draining trans-Tswana River (McCarthy 1983) and changes in its drainage patterns over time offer another putative causative agent in isolating geckos.

Concordant areas of endemism may be expected among groups of organisms that respond similarly to historical ecological conditions. In addition to Pachydactylus geckos, cordylid lizards (Broadley 1978; Jacobsen 1994; Mouton and van Wyk 1994; Bauer 1999) and scorpions (R.E. Griffin 1998; Prendini 2000, 2001b, 2003b, 2004; Prendini et al. 2003) are groups that show high substrate specificity. As such, they are also likely to have historically been subject to vicariance which tends to result in elevated rates of localized speciation, and thus increased diversity and endemism. Under ideal conditions the identification of multiple groups sharing similar distributions sets the stage for the application of analytical biogeographic approaches, such as cladistic biogeography (Humphries and Parenti 1999; Cotterill 2004). However, this has been hindered by two factors. First, until recently, the absence of robust species-level phylogenies for virtually all southern African biota has precluded any meaningful attempt at testable biogeographic hypotheses (Bauer and Lamb 2005). Second, and even more fundamental, most southern African animals remain in the discovery phase of alpha taxonomy, so that the identification of the units of consideration, whether for phylogenetic or biogeographic analyses, is tentative at best.

The Pachydactylus serval/weberi clade illustrates this well. Until the present study, only a few constituent taxa were recognized and many of the newly described forms remain known from just a few localities, mostly based on specimens collected relatively recently. This revision follows a broader phylogenetic analysis of the genus Pachydactylus (Bauer and Lamb 2005; Lamb and Bauer 2006) and brings the total number of named valid species in the Pachydactylus group (including Colopus, Elasmodactylus and Chondrodactylus) to 54. Although some issues of specific identity remain to be resolved and distributions for some taxa are still incompletely known, Pachydactylus is certainly the most diverse genus of southern African reptiles for which explicit phylogenetic hypotheses exist and holds the promise of being a key to elucidating biogeographic patterns in the subcontinent when combined with data from other groups that share overlapping areas of endemism and for which phylogenetic hypotheses exist, such as lacertids (Arnold 1991; Harris et al. 1998; Lamb \& Bauer 2003), some scincids (Daniels et al. 2002; Whiting et al. 2003), cordylids (Frost et al. 2001; Scott et al. 2004), and scorpions (Prendini 2001a; Prendini et al. 2003).

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## Literature Cited

Amos, B.. and A.R. Hoelzel. 1991. Long-term preservation of whale skin for DNA analysis. Reports of the International Whaling Commission, Special Issue 13:99-103.
ArNold, E.N. 1991. Relationships of South African lizards assigned to Aporosaura, Meroles and Pedioplanis (Reptilia: Lacertidae). Joumal of Natural History 25:783-807.
Auerbach, R.D. 1987. The Amphibians and Reptiles of Botswana. Mokwepa Consultants, Gaborone, Botswana. iii + [2] + 295 pp., 19 color pls.
AvISE, J.C. 1989. Gene trees and organismal histories: a phylogenetic approach to population biology. Evolution 43:1192-1208.
Axelrod, D.I., and P.H. Raven. 1978. Late Cretaceous and Tertiary vegetation history of Africa. Pages 79-130 in M.J.A. Werger, M.J.A. and A.C. van Bruggen, eds., Biogeography and Ecology of Southern Africa. Dr W. Junk Publishers, The Hague, The Netherlands.
Barbour. T., A.vD A. Loveridge. 1946. First supplement to typical reptiles and amphibians. Bulletin of the Museum of Comparative Zoology 96:57-214.
Bariatd. P.. S. Bethline. aidd H. Kolberg. 1998. Biodiversity of terrestrial and freshwater habitats. Pages 57-188 in P. Barnard, ed.. Biological Diversity in Namibia - A Country Study. Namibian National Biodiversity Task Force, Windhoek, Namibia.
BARTS. M. 2002. Die Dickfingergeckos des südlichen Afrikas. Teil II. Die Haltung und Vermehrung des Gebänderten Dickfingergeckos, Pachydactylus fasciatus Boulenger, 1888. Sauria 24(1):3-8.
Barts, M.. J. Boove, Avd F. Hulbert. 2001. Die Dickfingergeckos des südlichen Afrikas. Teil I. Die Haltung und Vermehrung des Tsodilo-Geckos. Pach dactylus tsodiloensis Haacke. 1966. Sauria 23(3):15-19.
Barts, M.. A.dD W.D. Hatcke. 1997. Zur Reptilienfauna der Tsodilo-Berge und angrenzender Gebiete in NWBotswana - Teil I. Testudines: Testudinidae; Sauria I. Sauria 19(1):3-12.

Barts, M., and W.D. Haacke. 2001. Gekkonidae. Pachydactylus tsodiloensis Haacke, 1966. Tsodilo Thicktoed Gecko. Maintenance and reproduction. African Herp News 33:11-12.
BaIER, A.M. 1990. Phylogeny and biogeography of the geckos of southern Africa and the islands of the western Indian Ocean: a preliminary analysis. Pages 275-284 in G. Peters and R. Hutterer, eds., Vertebrates in the Tropics. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany.
Baler. A.M. 1991. New reptile records for the Little Karoo. Journal of the Herpetological Association of Africa 39:18.
BaUER, A.M. 1999 [2000]. Evolutionary scenarios in the Pachydactylus-group geckos of southern Africa: new hypotheses. African Journal of Herpetology 48:53-62.
Bauer, A. M. and W.R. Branch. 1991. Notes on Pachydactylus fasciatus, a poorly known gecko from northern Namibia. Journal of the Herpetological Association of Africa 39:1-5.
Bauer, A.M., and W.R. Branch.. 2001 [2003]. The herpetofauna of the Richtersveld National Park and the adjacent northern Richtersveld, Northern Cape Province, Republic of South Africa. Herpetological Natural History 8:111-160.
Baler, A.M., W.R. Branch, and W.D. Haacke. 1993. The herpetofauna of the Kamanjab area and adjacent Damaraland, Namibia. Madoqua 18:117-145.
BaUER, A.M., and D.A. Good. 1996. Phylogenetic systematics of the day geckos, genus Rhoptropus (Reptilia: Gekkonidae), of south-western Africa. Journal of Zoology, London 238: 635-663.
BaUer, A.M., and R. Günther. 1991. An annotated type catalogue of the geckos (Reptilia: Gekkonidae) in the Zoological Museum, Berlin. Mitteilungen aus dem Zoologischen Museum in Berlin 67:279-310.
BaUer, A.M., And T. Lamb. 2002. Phylogenetic relationships among members of the Pachydactylus capensis group of southern African geckos. African Zoology 37:209-220.
Baver, A.M., and T. Lamb. 2003a. A new species of the Pachydactylus weberi group (Reptilia: Squamata: Gekkonidae) from the Waterberg Plateau, Namibia. Cimbebasia 19:1-12.
Baver, A.M. , and T. Lamb. 2003b. Distribution: Pachydactylus fasciatus Boulenger 1888. African Herp News 36:20-21.
Baler, A.M. , and T. Lamb. 2005. Phylogenetic relationships of southern African geckos in the Pachydactylus Group (Squamata: Gekkonidae). African Journal of Herpetology 54:105-129.
Baler, A.M., Lamb, T., and Branch, W.R. 1999. Additional records of uncommon Pachydactylus. African Herp News 30:2-4.
Baler, A.M., T. Lamb, and W.R. Branch. 2002. A revision of Pachydactylus scutatus (Reptilia: Squamata: Gekkonidae) with the description of a new species from northern Namibia. Proceedings of the California Academy of Sciences, ser. 4, 53:23-36.
BLAXTER, M.L. 2004. The promise of a DNA taxonomy. Philosophical Transactions of the Royal Society of London B 359:669-679.
Boulenger, G.A. 1910. A revised list of the South African reptiles and batrachians, with synoptic tables, special reference to specimens in the South African Museum, and descriptions of new species. Annals of the South African Museum 5:455-543.
Bollevger, G.A. 1888. On new and little-known South African reptiles. Annals and Magazine of Natural History (6)2:136-141.
Bollenger, G.A. 1890. First report on additions to the lizard collection in the British Musuem (Natural History). Proceedings of the Zoological Society of London 1890:77-87, pls. viii-xi.
Branch, W.R. 1981. An annotated checklist of the lizards of the Cape Province, South Africa. Annals of the Cape Provincial Museums (Natural History) 13:141-167.
Branch, W.R. 1988. Field Guide to the Snakes and Other Reptiles of Southern Africa. Struik Publishers, Cape Town, South Africa. 328 pp.
Bravch, W.R. 1990. The herpetofauna of the Cape Province, South Africa: new distribution records and zoogeography. Journal of the Herpetological Association of Africa 37:17-44.
Bravch, W.R. 1993. Southern African Snakes and Other Reptiles. A Photographic Guide. Struik Publishers, Cape Town, South Africa. 144 pp.
Branch, W.R. 1994a. Field Guide to the Snakes and Other Reptiles of Southern Africa, $2^{\text {nd }}$ edition. Struik Publishers, Cape Town, South Africa. 328 pp.

Branch, W.R. 1994b. Herpetofauna of the Sperrgebeit region of southern Namibia. Herpetological Natural History 2:1-11.
Branch, W.R. 1996. Citations and priority: a reply to van Dijk. African Herp News 25:27-28.
Branch, W.R. 1998. Field Guide to Snakes and Other Reptiles of Southern Africa, 3rd edition. Struik Publishers, Cape Town, South Africa. 399 pp.
Branch, W.R., and A.M. Bauer. 1995. Herpetofauna of the Little Karoo, Western Cape, South Africa with notes on life history and taxonomy. Herpetological Natural History 3:47-89.
Branch, W.R., A.M. Bauer, and D.A. Good. 1996. A review of the Namaqua gecko, Pachydactylus namaquensis (Reptilia: Gekkonidae) from southern Africa, with the description of two new species. South African Journal of Zoology 31:53-69.
Branch, W.R., and H.H. Braack. 1989. Reptiles and amphibians in the Karoo National Park: a surprising diversity. Journal of the Herpetological Association of Africa 36:26-35.
Broadley, D.G. 1977. A review of the northeastern forms of the Pachydactylus capensis complex (Sauria: Gekkonidae). Amoldia (Rhodesia) 8(18):1-19.
Broadley, D.G. 1978. A revision of the genus Platysaurus A. Smith (Sauria: Cordylidae). Occasional Papers of the National Museums and Monuments of Rhodesia B, Natural Sciences 6:129-185.
Broadley, D.G. 2003. Pachydactylus katanganus de Witte 1953, a species endemic to the Upemba National Park (Sauria: Gekkonidae). African Journal of Herpetology 52:69-70.
Brown, R.M., And A.C. Diesmos. 2001. Application of lineage-based species concepts to oceanic island frog populations: the effects of differing taxonomic philosophies on the estimation of Philippine biodiversity. Silliman Journal 42:133-162.
Burger, M. 1993. The herpetofauna of Anysberg Nature Reserve, Cape Province, South Africa. Journal of the Herpetological Association of Africa 42:1-12.
Coetzee, J.A. 1993. African flora since the Terminal Jurassic. Pages 37-61 in P. Goldblatt, ed., Biological Relationships Between Africa and South America. Yale University Press, New Haven, Connecticut, USA. vii $+[2]+630 \mathrm{pp}$.
Cotterill. F.P.D. 2004. Geomorphological influence on vicariant evolution in some African mammals in the Zambezi Basin: some lessons for conservation. Pages 1-26 in A.B. Plowman, ed., Ecology and Conservation of Small Antelope. Proceedings of an International Symposium on Duiker and Dwarf Antelope in Africa. Filander Verlag, Fürth, Germany.
Crowe, T. M. 1990. A quantitative analysis of patterns of distribution, species richness and endemism in southern African vertebrates. Pages 145-160 in G. Peters and R. Hutterer, eds., Vertebrates in the Tropics. Zoologiches Forschungsinstitut und Museum Koenig, Bonn, Germany.
Dann, S., and D. Hillenius. 1966. Catalogue of the type specimens of amphibians and reptiles in the Zoological Museum, Amsterdam. Beaufortia 13:117-144.
Daniels, S.R., N. Heideman, M. Hendricks, and B. Wilson. 2002. A molecular phylogeny for the South African limbless lizard taxa of the subfamily Acontinae (Sauria: Scincidae) with special emphasis on relationships within Acontias. Molecular Phylogenetics and Evolution 24:315-323.
De Queiroz. K. 1998. The general lineage concept of species. species criteria. and the process of speciation. Pages 57-75 in D.J. Howard and S.H. Berlocher, eds., Endless Forms: Species and Speciation. Oxford University Press, Oxford, UK.
De Wit. M.C.J. 1999. Post-Gondwana drainage and the development of diamond placers in western south Africa. Economic Geology 94:721-740.
Dingle. R.V.. t.dD Q.B. Hexdey. 1984. Mesozoic and Tertiary sediment supply to the western Cape Basin and paleodrainage systems in south-western Africa. Marine Geology 56:13-26.
Dollar. E.S.J. 1998. Palaeofluvial geomorphology in southern Africa: a review. Progress in Physical Geography 22:325-349.
Ferglson, J.W.H. 2002. On the use of genetic divergence for identifying species. Biological Journal of the Linnean Society 75:509-516.
FitzSimons. V.F. 1935. Notes on a collection of reptiles and amphibians made in the southern Kalahari, Bushmanland and Great and Little Namaqualand. Annals of the Transiaal Museum 15:519-550.
FitzSimovs. V:F. 1938. Transvaal Museum expedition to South-West Africa and Little Namaqualand, May to

August 1937. Reptiles and amphibians. Annals of the Transvaal Museum 19:153-209, pls. 2-3, 1 map.
FitzSinovs, V.F. 1941. Descriptions of some new lizards from South Africa and a frog from Southern Rhodesia. Annals of the Transvaal Museum 20:273-281, pl. 12.
FitzSimons, V.F. 1943. The Lizards of South Africa. Memoirs of the Transvaal Museum (1):i-xv + 1-528, + 24 pls + map.
Frost, D., D. Janies, P.le F.N. Mouton, and T. Titus. 2001. A molecular perspective on the phylogeny of the girdled lizards (Cordylidae, Squamata). American Museum Novitates (3310):1-10.
GIESS, W. 1971. A preliminary vegetation map of South West Africa. Dinteria 4:5-114.
Girard, F. 1997. Holidaying with herps in South Africa. African Herp News 26:13-15.
Girard, F. 2002. Maintenance and captive reproduction of two small, South African geckos, Pachydactylus geitje (Sparrman, 1778) and Pachydactylus weberi Roux, 1907. Gekko 3(1):14-18.
Goudie, A.S. 2005. The drainage of Africa since the Cretaceous. Geomorphology 67:437-456.
Griffiv, M. 1998. Reptile diversity. Pages 148-154 in P. Barnard, ed., Biological Diversity in Namibia - A Country Study. Namibian National Biodiversity Task Force, Windhoek, Namibia.
Griffin, M. 2000a. Annotated checklist of amphibians, reptiles and mammals of the Brandberg, central Namib Desert, Namibia. Cimbebasia Memoirs 9:69-89.
Griffin, M. 2000b. The species diversity, distribution and conservation of Namibian reptiles: a review. Namibia Wissenschaftliche Gesellschaft Journal 48:116-141.
Griffin, M. 2003. Annotated Checklist and Provisional National Conservation Status of Namibian Reptiles. Namibia Scientific Society, Windhoek. [2] + 169 pp.
Griffin, R.E. 1998. Species richness and biogeography of non-acarine arachnids in Namibia. Biodiversity and Conservation 7:467-481.
H.acke. W.D. 1965. Additional notes on the herpetology of South West Africa with descriptions of two new subspecies of geckos. Cimbebasia (11):1-40.
Htacke, W.D. 1966. A new gekko (Sauria, Geckonidae) from Bechuanaland. Arnoldia (Rhodesia) 2(25):1-7.
Hacke, W.D. 1968. A Taxonomic and Ecological Study of the Burrowing Geckos of Southern Africa. M.Sc. Thesis, University of Pretoria, Pretoria, South Africa.
Haacke, W.D. 1976. The burrowing geckos of southern Africa, 5 (Reptilia: Gekkonidae). Annals of the Transvaal Museum 30:71-89.
HaAcke, W.D. 1982. Distribution patterns of reptiles as indicators of geomorphological events in the Namib Desert. Pages 225-226 in J.A. Coetzee and E.M. van Zinderen Bakker, eds., Palaeoecology of Africa and the Surrounding Islands. A.A. Balkema, Rotterdam, The Netherlands.
HAAG\ER, G.V. 1991. Notes on a herpetological collecting trip to Namibia (24 October to 3 November 1990). African Herp News 15:36-39.
HaAGIER, G.V., AND W.R. Branch. 1995. Notes on a herpetological collecting trip to the southern Great Karoo and adjacent Little Karoo. African Herp News 24:9-15.
Harris, D.J., E.N. Arnold, and R.H. Thomas. 1998. Rapid speciation, morphological evolution, and adaptation to extreme environments in South African sand lizards (Meroles) as revealed by mitochondrial gene sequences. Molecular Phylogenetics and Evolution 10:37-48.
Hasegawa, M., H. Kishino, and T. Yano. 1985. Dating the human-ape splitting by a molecular clock of mitochondrial DNA. Journal of Molecular Evolution 22:160-174.
Hebert, P.D.N., A. Cywinska, S.L. Ball, and J.R. deWaard. 2003. Biological identifications through DNA barcodes. Proceedings of the Royal Society of London B 270:33-321.
Hewrtt, J. 1910. A key to the South African species* of Geckonidae, Scincidae, Gerrhosauridae, and Lacertidae, together with some notes on the specific characters and a brief summary of the known facts of their distribution. Annals of the Transvaal Museum 2:77-115.
Hewitt, J. 1911. Records of South African Lacertilia and Amphibia. Addenda and Corrigenda. Annals of the Transvaal Museum 3:42-55.
Hewitt, J. 1913. Description of Heleophryne natalensis, a new batrachian from Natal; and notes on several South African batrachians and reptiles. Annals of the Natal Museum 2:475-484, pl. XXXIX.
Hewitt, J. 1927. Further descriptions of reptiles and batrachians from South Africa. Records of the Albany Museum 3:371-415, pls. XX-XXIV.

Hewrit, J. 1932. Some new species and subspecies of South African batrachians and lizards. Annals of the Natal Museum 7:105-128, pl. VI.
Hewitt, J. 1935. Some new forms of batrachians and reptiles from South Africa. Records of the Albany Museum 4:283-357, pls. XXVII-XXXVI.
Hollingsworth, B.D. 1998. The systematics of chuckwallas (Sauromalus) with a phylogenetic analysis of other iguanid lizards. Herpetological Monographs 12:38-191.
Huelsenbeck, J.P., and F.R. Ronquist. 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17:754-755.
Humphries, C.J., and L.R. Parenti. 1999. Cladistic Biogeography, $2^{\text {nd }}$ edition. Oxford University Press, Oxford, UK. xi + 187 pp .
International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature, Fourth Edition. International Trust for Zoological Nomenclature, London. xxix +306 pp.
Irish, J. 1994. The biomes of Namibia, as determined by objective categorisation. Navorsinge van die Nasionale Museum Bloemfontein 10:549-592.
Irish, J. 2002. Namibian Mountains: Biodiversity Potential Based on Topography. Report to the Mountain Working Group of the National Biodiversity Task Force, Windhoek, Namibia. 42 pp.
Jacobsen. N.H.G. 1994. The Platysaurus intermedius complex (Sauria: Cordylidae) in the Transvaal, South Africa, with descriptions of three new taxa. South African Journal of Zoology 29:132-143.
Joger, U. 1985. The African gekkonine radiation - preliminary phylogenetic results based on quantitative immunological comparisons of serum albumins. Pages 479-494 in K.-L. Schuchmann, ed., Proceedings of the International Symposium on African Vertebrates. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany.
Johns, G.C., and J.C. Avise. 1998. A comparative summary of genetic distances in the vertebrates from the mitochondrial cytochrome $b$ gene. Molecular Biology and Evolution 15:1481-1490.
Jürgens, N. 1991. A new approach to the Namib region. I: Phytogeographic subdivision. Vegetatio 97:21-38.
Kimura, M. 1980. 1980. A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16:111-120.
Kluge, A.G. 1991. Checklist of gekkonoid lizards. Smithsonian Herpetological Information Service (85):1-35.
Kluge, A.G. 1993. Gekkonoid Lizard Taxonomy. International Gecko Society, San Diego, California, USA. 245 pp .
Kluge, A.G. 2001. Gekkotan lizard taxonomy. Hamadryad 26:1-209.
Kllge, A.G., a.dd R.A. Nussbatil. 1995. A review of African-Madagascan gekkonid lizard phylogeny and biogeography (Squamata). Misceluneous Publications of the Museum of Zoology: University of Michigan (183):1-20.

Kramer, E. 1979. Typenkatalog der Echsen im Naturhistorischen Museum Basel (BM), Stand 1978. Revue Suisse de Zoologie 86:159-166.
Lamb. T.. a.dd A.M. Baler. 2000. Systematics of the Pachydactilus rugosus complex of southern African geckos (Squamata: Gekkonidae). African Zoology 35:55-67.
Lamb, T.. A.Md A.M. Baler. 2001. Mitochondrial phylogeny of Namib day geckos (Rhoptropus) based on cytochrome b and 16S rRNA sequences. Copeia 2001:775-780.
Lamb, T., a.jd A.M. Bayer. 2002. Phylogenetic relationships of the large-bodied members of the African lizard genus Pachydacthlus (Reptilia: Gekkonidae). Copeia 2002:586-596.
L.amb, T.. A.ID A.M. Bater. 2006. Footprints in the sand: independent reduction of subdigital lamellae in the Namib-Kalahari burrowing geckos. Proceedings of the Roval Society of London B 273:855-864.
Lairrexce. R.F. 1929. The reptiles of S.W.A. Journal of the South West African Scientific Society 2:13-27.
Lawrence, R.F. 1936. The prostigmatic mites of South African lizards. Parasitology 28:1-39.
Lawrexce. R.F. 1951. New parasitic mites from South African lizards. Annals of the Transvaal Museum 21:447-459
Levitox. A.E., R.H. Gibbs. Jr.. E. Heal.. and C.E. Daiwson. 1985. Standards in herpetology and ichthyolog.y: Part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802-832.
Loveridge. A. 19+4. New geckos of the genera Afroedura. new genus. and Pachydactilus from Angola.

American Museum Novitates (1254):1-4.
Loveridge. A. 1947. Revision of the African lizards of the Family Gekkonidae. Bulletin of the Museum of Comparative Zoology 98:1-469, pls. 1-7.
Maggs. G.L., P. Craten, and H.H. Kolberg. 1998. Plant species richness, endemism, and genetic resources in Namibia. Biodiversity and Conservation 7:435-446.
MAyDEV. R.L. 1997. A hierarchy of species concepts: the denouement in the saga of the species problem. Pages 381-424 in M.F. Claridge, H.A. Dawah and M.R. Wilson, eds., Species: The Units of Biodiversity. Chapman and Hall, New York, New York, USA.
Mayer, W., and Richter, K. 1990. Die Wüstenrenner-Eidechsen Namibias - Vorkommen, Pflege und Zucht. Herpetofauna 12(66):21-30.
McCaRTHY, T.S. 1983. Evidence for the former existence of a major, southerly flowing river in Griqualand West. Transactions of the Geological Scoiety of South Africa 86:37-49.
Mclachlan, G. R., and J. M. Spence. 1966. The genus Pachydactylus (Part 1). Annals of the Cape Provincial Museums 5:149-156.
Mertevs, R. 1955. Die Amphibien und Reptilien Südwestafrikas, aus den Ergebnissen einer im Jahre 1952 ausgeführten Reise. Abhandlungen der Senckenbergischen naturforschenden Gesellschaft (490):1-172.
Mertens, R. 1971. Die Herpetofauna Südwest-Afrikas. Abhandlungen der Senckenbergischen naturforschenden Gesellschaft (529):1-110.
Methlen, P.A., and J. Hewitt. 1914. The Percy Sladen Memorial Expedition to Great Namaqualand, 1912-1913. Records and descriptions of the Reptilia and Batrachia. Annals of the Transvaal Museum 4:118-145, pl. 14.
Meyer, A., T.D. Kocher, P. Basasibwaki, and A.C. Wilson. 1990. Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial DNA sequences. Nature 347:550-553.
Michels, J.P., And A.M. Baler. 2004. Some corrections to the scientific names of amphibians and reptiles. Bonner Zoologische Beiträge 52:83-94.
Movard, A. 1931. Reptiles. Mission Scientifique Suisse dans l'Angola, Résultats Scientifiques. Bulletin de la Société Neuchâteloise des Sciences Naturelles 55:89-111.
Monard, A. 1937. Contribution à l'herpétologie d'Angola. Arquivos do Museu Bocage 8:19-154.
Moon, B.P., And G.F. Dardis. 1988. The Geomorphology of Southern Africa. Southern Book Publishers, Johannesburg, South Africa. 320 pp.
Moore, W.S. 1995. Inferring phylogenies from mtDNA variation: mitochondrial-gene trees versus nucleargene trees. Evolution 49:718-726.
Molton, P. le F.N., and H. Van Wyk. 1994. Taxonomic status of geographic isolates in the Cordylus minor complex (Reptilia: Cordylidae): a description of three new species. Journal of the Herpetological Association of Africa 43:6-18.
Mcicina, L., and M.C. Rutherford, eds. 2004. Vegetation Map of South Africa, Lesotho and Swaziland: Shapefiles of Basic Mapping Units. Beta version 4.0, February 2004. South African National Biodiversity Institute, Cape Town, South Africa.
Nyla.dier, J.A.A. 2004. MrModelTest 2.0. Program distributed by the author, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.
PARKER, H.W. 1936. Dr. Karl Jordan's expedition to south-west Africa and Angola: herpetological collections. Novitates Zoologicae 40:115-146.
Partridge, T.C., and R.R. Maud. 2000. Macro-scale geomorphic evolution of southern Africa. Pages 3-18 in T. Partridge, and R.R. Maud, eds., The Cenozoic of Southern Africa. Oxford University Press, Oxford, U.K.

Peters, W.C.H. 1867. Über eine Sammlung von Flederthieren und Amphibien aus Otjimbingue in Südwestafrica, welche Hr. Missionär Hahn dem zoologischen Museum zugesandt hat. Monatsberichte der königlichen Akademie der Wissenschaften zu Berlin 1867:234-237, 1 pl.
Peters, W.C.H. 1870. Beitrag zur Kenntniss der herpetologischen Fauna von Südafrika. Monatsberichte der königlichen Akademie der Wissenschaften zu Berlin 1870:110-115, 1 pl.
Prendin, L. 2001a. Phylogeny of Parabuthus (Scorpiones, Buthidae). Zoologica Scripta 30:13-35.
Prevdini, L. 2001b. Substratum specialization and speciation in southern African scorpions: the Effect Hypothesis revisited. Pages 113-138 in V. Fet and P.A. Selden, eds., Scorpions 2001: In Memoriam Gary
A. Polis. British Arachnological Society, Manchester, UK.

Prendini, L. 2003a. Revision of the genus Lisposoma Lawrence, 1928 (Scorpiones: Bothriuridae). Insect Systematics and Evolution 34:241-264.
Prendin, L. 2003b. Discovery of the male of Parabuthus muelleri, and implications for the phylogeny of Parabuthus (Scorpiones: Buthidae). American Museum Novitates (3408):1-24.
Prendini, L. 2004. The systematics of southern African Parabuthus Pocock (Scorpiones, Buthidae): revisions to the taxonomy and key to the species. Journal of Arachnology 32:109-186.
Prendint, L., T.M. Crowe, and W.C. Wheeler. 2003. Systematics and biogeography of the family Scorpionidae (Chelicerata: Scorpiones), with a discussion on phylogenetic methods. Invertebrte Systematics 17:185-259.
Röll, B. 2001. Mikrostrukturen der Eischalen von Geckos (Sauria: Gekkonoidea). Gekkota 3:74-98.
Rösler, H. 2000. Kommentierte Liste der rezent, subrezent und fossil bekannten Geckotaxa (Reptilia: Gekkonomorpha). Gekkota 2:28-153.
Rösler, H. 2005. Vermehrung von Geckos. Grundlagen - Anleitungen - Erfahrungen. Herpeton, Offenbach. 270 pp .
Roux, J. 1907. Beiträge zur Kenntnis der Fauna von Süd-Afrika. Zoologische Jahrbücher, Abteilung für Systematik 25:403-444, pls. 14-15.
Russell, A.P. 1972. The Foot of Gekkonid Lizards: A Study in Comparative and Functional Anatomy. Ph.D. Dissertation. University of London, London, UK.
Schneider, I. 1998. Waterberg Plateau Park Namibia, updated edition. Shell Namibia, Windhoek, Namibia. 64 pp.
Schultze, L.S. 1907. Aus Namaland und Kalahari. Bericht an die Kgl. preuss. Akademie der Wissenschaften zu Berlin ïber eine Forschungsreise im westlichen und zentralen Sïdafrika, ausgeführt in den Jahren 1903-1905. G. Fischer, Jena, Germany. xiv +752 pp., XXV pls.
Sclater, W.L. 1898. List of the reptiles and batrachians of South Africa, with descriptions of new species. Annals of the South African Museum 1:95-111, pl. V.
Scott, I.A.W.. J.S. Keogh. and M.J. Whitivg. 2004. Shifting sands and shifty lizards: molecular phylogeny and biogeography of African flat lizards (Platysaurus). Molecular Phylogenetics and Evolution 31:618-629.
Selfer. H. 1991. Keeping and Breeding Geckos. TFH Publications. Inc.. Neptune City, New Jersey. 189 pp.
SIESSER, W.G. 1978. Aridification of the Namib Desert: evidence from oceanic cores. Pages 105-113 in E.M. van Zinderen Bakker, ed., Antarctic Glacial History and World Palaeoenvironments. A.A. Balkema, Rotterdam. The Netherlands.
Siesser W.G. 1980. Late Miocene origin of the Benguela upwelling system off northern Namibia. Science 208:283-285.
Simmons. R.E., M. Griffin, R.E. Griffin. E. Marais, axd H. Kolberg. 1998. Endemism in Namibia: patterns, processes and predictions. Biodiversity and Conservation 7:513-530.
Sites, J.W., Jr., and J.C. Marshall. 2003. Delimiting species: a Renaissance issue in systematic biology. Trends in Ecology and Evolution 18:462-470.
Sites, J.W., Jr., and J.C. Marshall. 2004. Operational criteria for delimiting species. Annual Review of Ecology and Systematics 35:199-227.
Stervfeld. R. 1911a. Zur Herpetologie Südwestafrikas. Mitteilungen aus dem Zoologischen Museum in Berlin 5:393-411.
Ster..feld. R. 1911b. Die Reptilien (außer den Schlangen) und Amphibien von Deutsch- Südwestafrika. Die Fauna der deutschen Kolonien IV (2):i-iv $+1-65,1$ map.
Stel... W.. a.d. A. J.L. Mitchell. 1967. Two new gekkos from South West Africa. Cimbebasia (21):9-21.
StLart. C.T. 1980. An annotated preliminary list of amphibians and reptiles known to occur in the Namib Desert Park, Namibia. Journal of the Herpetological Association of Africa 24:4-13.
Thomis. D.S.G. A.vd P.A. Sh.ilw. 1993. The evolution and characteristics of the Kalahari, southern Africa. Journal of Arid Environments 25:97-108.
Thompson, J.D.. T.J. Gibson. F. Plewniak. F. Jeanmolgin. and D. G. Higgins. 1997.The Clustal X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic

Acids Research 24:4876-4882.
Tyson, P.D. 1986. Climatic Change and Variability in Southern Africa. Oxford University Press, Cape Town, South Africa. ix +220 pp .
Trison. P.D... and T.C. Partridge. 2000. Evolution of Cenozoic climate. Pages 371-387 in T.C. Partridge and R.R. Maud, eds., The Cenozoic of Southern Africa. Oxford University Press, Oxford, U.K.

Vav den Elzen, P. 1978. Observations sur l'herpétofaune du Waterberg (Namibie). Bonner Zoologische Beiträge 29:171-182.
Van Duk, D.E. 1996. Citations: the description of Heleophryne by W.L. Sclater, and other citations. African Herp News 25:26.
van Tuill, L. 1995. Revised catalogue of the type specimens of recent amphibians and reptiles in the "Zoölogisch Museum" University of Amsterdam, the Netherlands. Bulletin Zoölogisch Museum, Universiteit van Amsterdam 14:125-144.
van Wyk, A.E., and G.F. Smith. 2001. Regions of Floristic Endemism in Southern Africa. Umdaus Press, Hatfield, South Africa. viii + 199 pp.
Visser. J. 1984. Tierboskat-geitjes kies klipperige woonplek. Akkedisse van Suider-Afrika 7. Landbouweekblad, 27 April 1984:48-49, 51, 53.
Volk, O.H. 1966. Die Florengebiete von Südwestafrika. Journal der Südwest Afrikanische Wissenschaftliche Gesellschaft 20:25-58.
Watson, D.M. 2005. Diagnosable versus distinct: evaluating species limits in birds. BioScience 55:60-68.
Welch, K.R.G. 1982. Herpetology of Africa: A Checklist and Bibliography of the Orders Amphisbaenia, Sauria and Serpentes. Robert E. Krieger Publishing Co., Malabar, Florida. x +293 pp.
Welch, K.R.G. 1994. Lizards of the World. A Checklist. 1. Geckos. R \& A Research and Information Limited, Taunton, UK. 165 pp.
Wermuth, H. 1965. Liste der rezenten Amphibien und Reptilien, Gekkonidae, Pygopodidae, Xantusiidae. Das Tierreich 80. Walter de Gruyter, Berlin. xxii +246 pp.
Werner, F. 1910. Reptilia et Amphibia. Pages 279-370, pls. VI-XI in L. Schultze, ed., Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrika ausgeführt in den Jahren 1903-1905. Gustav Fischer, Jena, Germany.
Werver, F. 1915. Reptilia und Amphibia. Pages 323-376, pl. VII in W. Michaelsen, ed., Beiträge zur Kenntnis der Land- und Sï̈ßwasserfauna Deutsch-Südwestafrikas. Ergebnisse der Hamburger deutsch-südwestafrikanischen Studienreise 1911. L. Friedrichsen \& Co., Hamburg, Germany.
Whiting, A., A.M. BaUER, And J.W. Sites, Jr. 2003. Phylogenetic relationships and "omh inc- in sub-Saharan African scincine lizards (Squamata: Scincidae). Molecular Phylogenetics and Evolution 29:582-598.
Wiens, J.J., And T.A. Penkrot. 2002. Delimiting species using DNA and morphological variation and discordant species limits in spiny lizards (Sceloporus). Systematic Biology 51:69-91.
WIENS, J.J., AND M.R. SERVEDIO. 2000. Species delimitation in systematics: inferring diagnostic differences between species. Proceedings of the Royal Society of London B 267:631-636.
Woodrlff, F., S.M. Savin, and R.G. Douglas. 1981. Miocene stable isotope record: a detailed deep Pacific Ocean study and its paleoclimatic implications. Science 212:665-668.

## Appendix

GenBank accession numbers for cyt $b$ sequences used in this study.

| Species | Museum number | Accession number | Species | Museum <br> number | Accession number |
| :---: | :---: | :---: | :---: | :---: | :---: |
| P. affinis | AMB 6157 | AY 123414 | P. montanus | PEM R 5775 | DQ349147 |
| P. capensis | CAS 214501 | AF449133 |  | NMNW R 8832 | DQ349150 |
| P. carinatus | CAS 193365 | DQ349164 |  | NMNW R. 8833 | DQ349151 |
|  | CAS 231879 | DQ349162 |  | NMNW R 8841 | DQ349148 |
|  | CAS 231880 | DQ349163 |  | NMNW R 8846 | DQ349153 |
|  | AMB 4610 | DQ349165 |  | NMNW R 8874 | DQ349141 |
| P. fasciatus | CAS 193681 | AF449128 |  | NMNW R 8875 | DQ349142 |
| P. griffini | CAS 186294 | DQ349166 | P. purcelli | CAS 198294 | DQ349159 |
| P. kobosensis | CAS 223903 | DQ349187 |  | CAS 201844 | DQ349160 |
|  | CAS 223904 | DQ349188 |  | CAS 231887 | DQ349161 |
|  | CAS 223905 | DQ349189 | P. reconditus | CAS 231886 | DQ349182 |
| P. monicae | CAS 193406 | DQ349180 |  | NMNW R 10493 | DQ349181 |
|  | CAS 193418 | DQ349178 | P. robertsi | NMNW R 6697 | DQ349185 |
|  | CAS 200034 | DQ349179 | P. serval | NMNW R 8857 | DQ349167 |
|  | CAS 200079 | DQ349177 |  | NMNW R 8858 | DQ349168 |
| P. montanus | AMB 4900 | DQ349155 | P. tsodiloensis | MB, No number | AY123408 |
|  | AMB 38332 | DQ349143 | P. waterbergensis | MB, No number | DQ349176 |
|  | CAS 176252 | DQ349139 | P. Weberi | AMB 4309 | DQ349170 |
|  | CAS 176256 | DQ349145 |  | CAS 186368 | DQ349172 |
|  | CAS 176258 | DQ349144 |  | CAS 186371 | DQ349173 |
|  | CAS 201864 | DQ349149 |  | CAS 199997 | DQ349175 |
|  | CAS 201865 | DQ349152 |  | CAS 199998 | DQ349174 |
|  | CAS 201867 | DQ349140 |  | CAS 200056 | DQ349171 |
|  | CAS 201870 | DQ349154 |  | CAS 206754 | DQ349169 |
|  | CAS 203498 | DQ3+9158 | P. wemeri | MB, No number | DQ349183 |
|  | CAS 231884 | DQ349157 |  | MCZ R 183707 | DQ349184 |
|  | CAS 231885 | DQ3+9156 | P. sp. "Augrabies" | MB, No number | DQ349186 |
|  | PEM R 5774 | DQ3+9146 |  |  |  |

 referred to; square brackets [ I indicate implied synonymy based on distribution maps provided.

| liaxell | $\begin{gathered} \text { Fit:Simems } \\ 194.3 \end{gathered}$ | Lenervider $1947$ | $\begin{gathered} \text { Mhertens. } \\ 195.5 \end{gathered}$ | Wermuth 1965 | Matlatilan \& Spence 1966 | Mertens 1971 | Branch 1981 | Welch 1982 | Visser 1984 | Branch 1988, 1998 | $\begin{aligned} & \text { Kluge } 1991 . \\ & 1993,2001 \end{aligned}$ | Rösler 200日 | $\begin{gathered} \text { Ciriffin } \\ 2003 \end{gathered}$ | This Study |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| P. fousciuths Boukenger, ISSS | P. fowcidus | P. fusciatus | P. fasciutus | P. fusciatus | N | P. fusciatus | P. fascialus | P. fasciatus | N | P. fasciatus | P. fasciatus | P. fasciafus | P. fascialus | $P$ fasciatus |
| P. weberi Roux. 1907 | P. wederi | p. weberi | P. weberi | P. wetheri | N | P. weberi | P. weberi | P. weberi | P. weberi | P. weberi | P.weheri weberi | P. weheri weberi | P. weberi | P. weberi |
| P. serval Werner. 1910 | P. serval | P. serval | P. serral | P. serral | P. serval serval | P. serval soroal | P. serval serval | P. serval s.ened | P. serval served | P. serval servel | P. senval senval | $P$. serval servel | P. serval serval | P. serval |
| P. pureelli Boulenger. 1910 | P. purrelli | P. pureelli | P. purcelli | P. purcelli | P. serval purrelli | P. serval puicelli | P. serval purnelli | P. serval purcelli | P. serval purcelli | P. serval purcelli | P. serval purcelli | P. serval purcelli | P. serval purcelli | P. purcelli |
| P. porrdus Sternield. 1911 | syn. P. purcelli | syn. P. purcelli | syn. P. purcelli | syn P. purcelli | N | N | N | N | N | N | syn. P. serval | N | N | syn. P. purcelli |
| P. montames Methuen \& Hewitt. 1914 | P. montames | syn. P. serval | syn. P. semal | syn. P. serval | syn. P. serval serval | N | syn. P. serval serval | syn. P. serval | N | N | syn. P. scrual | N | N | P. montanus |
| P. capensis gariesensis Hewit, 1932 | P. weberi gariesensis | P. weheri gariesensis | N | P. weberi gariesensis | N | N | syn. P. weheri | P. weberi gariesensis | N | N | syn. P. weheri | N | N | syn. P. weberi |
| P. capensis werneri Hewtt, 1935 | P. werneri | P. weheri wemeri | P. nerneri | P. werneri | N | P. werneri | P. weberi wement | P. weberi werner | [syn. P. welderi] | [syn. $P$. weheri] | P. weberi wernert | P. weberi werneri | P. weheri werneri | P. werneri |
| P. montamus omscepensi, Hewitt. 1935 | P. montanus onscepensis | syn. P. serval | syn. P. serval | syn. P. serval | P. serval onscepensis | P. serval onscepensis | P. serval onscepensis | P. serval onscepensis | P. serval onscepensis | P. serval onscepensis | P. serval onscepensis | P. serval onscepensis | P. serval onscepensis | P. montanus |
| P. kobosensis FitzSimons. 1938 | P. kobosensis | P. kobosensis | P. kobosensis | P. kobosensis | N | P. kobosensis | N | P. kobosensis | P. kobosensis | N | P. kobosensis | P. kobosensis | P. kobosensis | sP. kobosensis |
| P. robertsi FinsSimons, 1938 | P. robertsi | P. scutantis robertsi | P. scutatus robertsi | P. scutatus mobertsi | N | P. scutatus robertsi | N | P. scutatus robertsi | N | N | P. scutatus robertsi | P. scutatus robertsi | P. mbertsi | P. robertsi |
| P. weheri acmminatus FiaSimons. 1941 | P. weheri cutuminatus | P. weberi actuminattus | P. weberi acuminatus | P. weberi acuminatus | N | P. weberi actuminaths | P. weberi acuminatus | P. weberi acuminatus | [syn. $P$ weberil | [syn. $P$. weberi] | P. weberi acuminatus | P. weberi acuminatus | P. weberi acuminatus | P. acuminatus |
| P. Isodiloensis Haacke. 1966 |  |  |  |  |  | N | N | N | N | P. sodiloensis | P. Asodiloensis | P. Isodiloensis | N | P. Asodilochsis |
| P. serval sansteyni McLachlan \& Spence, 1967 |  |  |  |  |  | P. serval sansteyni | N | P. serval sansteyni | N | P. sansteyni | P. sansteyni | P. sansteyni | P. sansteyni | P. samsteynae |
| P. waterbergensis Bauer \& Lamb, 2003 |  |  |  |  |  |  |  |  |  |  |  |  |  | P. naterver gensis |

Table 2. Mensural data for the adult types of Pachydactylus reconditus, sp nov. Abbreviations as in Materials and methods. All measurements in mm.

|  | TM | TM |  |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | TM <br> holotype | TM <br> paratype | CAS <br> paratype | CMNW <br> 231886 <br> paratype | NM 3462 <br> paratype | NMNW <br> R 3465 <br> paratype | NMNW <br> R 3745 <br> paratype | NMNW <br> R 10493 <br> paratype |
| Sex | female | male | juv. female | female | male | juvenile | juvenile | female |
| SVL | 42.2 | 44.7 | 30.3 | 42.3 | 38.7 | 25.6 | 28.7 | 37.9 |
| ForeaL | 5.6 | 5.9 | 4.0 | 5.5 | 5.3 | 3.7 | 3.8 | 5.0 |
| CrusL | 6.5 | 7.1 | 4.6 | 6.0 | 5.8 | 3.9 | 4.5 | 6.1 |
| TailL | 16.6 | 39.8 | 20.2 | 49.5 | 44.6 | 25.0 | 32.5 | 44.1 |
| (regen.) | broken | 31.4 | broken | 14.7 | broken | N/A | N/A | 17.9 |
| TailW | 5.2 | 4.3 | 2.1 | 4.2 | 4.1 | 1.9 | 2.9 | 3.1 |
| TrunkL | 18.5 | 18.3 | 12.0 | 17.4 | 16.7 | 8.2 | 11.0 | 13.4 |
| HeadL | 12.3 | 13.1 | 9.1 | 13.0 | 10.4 | 7.3 | 8.5 | 12.0 |
| HeadW | 7.8 | 8.5 | 5.7 | 8.4 | 8.1 | 5.7 | 5.7 | 7.8 |
| HeadH | 4.5 | 4.8 | 3.1 | 4.2 | 4.6 | 2.9 | 3.2 | 4.2 |
| OrbD | 3.0 | 3.2 | 2.2 | 3.1 | 2.7 | 2.0 | 2.7 | 2.7 |
| EyeEar | 3.1 | 3.5 | 2.5 | 3.1 | 3.0 | 1.9 | 2.0 | 3.2 |
| SnEye | 4.2 | 4.6 | 3.0 | 4.4 | 4.0 | 2.8 | 3.0 | 3.9 |
| NarEye | 3.1 | 3.4 | 2.2 | 3.1 | 3.0 | 1.7 | 2.1 | 3.2 |
| Interorb | 2.9 | 3.0 | 1.9 | 2.8 | 3.1 | 2.2 | 2.0 | 2.7 |
| EarL | 0.8 | 0.8 | 0.5 | 0.8 | 1.1 | 0.7 | 0.6 | 0.8 |
| Internar | 1.1 | 1.3 | 0.9 | 1.2 | 1.2 | 0.8 | 0.9 | 1.0 |

Table 3. Mensural data for the types of Pachydactylus monicae, sp. nov. Abbreviations as in Materials and methods. All measurements in mm.

|  | $\begin{gathered} \text { CAS } \\ 200034 \\ \text { holotype } \end{gathered}$ | CAS $193406$ <br> paratype | CAS 193417 paratype | CAS $200079$ <br> paratype | PEM <br> R 7626 <br> paratype | PEM <br> R 11952 <br> paratype | $\begin{gathered} \text { TM } \\ 28297 \\ \text { paratype } \end{gathered}$ | $\begin{gathered} \mathrm{TM} \\ 33806 \end{gathered}$ <br> paratype | $\begin{gathered} \text { TM } \\ 36367 \\ \text { paratype } \end{gathered}$ | $\begin{gathered} \text { TM } \\ 41852 \\ \text { paratype } \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sex | male | male | juv. fem? | uv. male | female | female | male | female | female | male |
| SVL | 44.1 | 42.1 | 28.5 | 31.1 | 45.7 | 47.8 | 42.6 | 50.3 | 47.9 | 42.9 |
| ForeaL | 6.3 | 6.1 | 3.8 | 4.6 | 6.5 | 6.9 | 5.6 | 6.4 | 6.9 | 6.2 |
| CrusL | 7.3 | 7.8 | 4.8 | 5.4 | 7.8 | 7.8 | 7.0 | 8.3 | 7.7 | 7.6 |
| TailL | 45.1 | 28.2 | 25.7 | 34.1 | 2.5 | 47.6 | 29.8 | 39.2 | 43.0 | 28.1 |
| (regen.) | 9.3 | 2.6 | broken | N/A | broken | 8.8 | 26.4 | 2.0 | 13.0 | 15.5 |
| TailW | 4.2 | 4.2 | 2.2 | 2.7 | N/A | 4.4 | 4.4 | 5.5 | 4.0 | 4.6 |
| TrunkL | 18.5 | 15.7 | 12.5 | 14.1 | 19.4 | 20.3 | 18.6 | 22.1 | 20.6 | 18.2 |
| HeadL | 13.8 | 12.9 | 8.8 | 10.0 | 13.3 | 15.0 | 11.9 | 13.6 | 12.9 | 12.7 |
| HeadW | 8.4 | 8.0 | 6.1 | 6.4 | 8.9 | 8.9 | 7.6 | 9.4 | 8.9 | 8.2 |
| HeadH | 5.0 | 4.5 | 3.3 | 4.0 | 5.2 | 5.3 | 5.0 | 6.4 | 6.0 | 5.0 |
| OrbD | 3.3 | 3.1 | 2.2 | 2.6 | 3.2 | 3.6 | 3.2 | 3.1 | 3.2 | 3.0 |
| EyeEar | 3.3 | 3.3 | 2.7 | 2.9 | 3.2 | 3.7 | 3.1 | 4.0 | 4.0 | 3.4 |
| SnEye | 4.6 | 4.4 | 3.4 | 3.9 | 4.8 | 5.1 | 4.9 | 5.2 | 4.8 | 4.3 |
| NarEye | 3.6 | 3.5 | 2.4 | 2.7 | 3.6 | 4.0 | 3.4 | 4.0 | 3.7 | 3.4 |
| Interorb | 3.3 | 3.1 | 2.1 | 2.6 | 3.1 | 3.2 | 3.4 | 3.9 | 3.6 | 3.2 |
| EarL | 1.1 | 1.1 | 0.5 | 0.8 | 1.0 | 0.8 | 0.8 | 0.9 | 0.9 | 0.5 |
| Internar | 1.3 | 1.2 | 1.0 | 1.0 | 1.4 | 1.2 | 1.1 | 1.4 | 1.3 | 1.1 |

Table 4. Mensural data for the adult types of Pachydactylus griffini, sp. nov. See Variation section for information regarding juvenile paratypes. Abbreviations as in Materials and methods. All measurements in mm.

|  | CAS 125855 | CAS 125854 | CAS 186294 MCZ R 163286 |  |
| :--- | :---: | :---: | :---: | :---: |
|  | holotype | paratype | paratype | paratype |
| Sex | female | female | male | male |
| SVL | 30.3 | 35.5 | 39.4 | 34.8 |
| ForeaL | 4.8 | 4.2 | 5.2 | 4.9 |
| CrusL | 5.1 | 5.4 | 6.4 | 5.2 |
| TailL | 26.7 | 2.2 | 2.3 | 27.3 |
| $\quad$ (regen.) | 3.3 | broken | broken | 24.0 |
| TailW | 2.5 | N/A | N/A | 3.8 |
| TrunkL | 13.8 | 14.3 | 16.3 | 15.9 |
| HeadL | 8.7 | 10.6 | 11.5 | 10.0 |
| HeadW | 6.0 | 6.3 | 8.0 | 7.4 |
| HeadH | 3.2 | 3.3 | 3.9 | 4.3 |
| OrbD | 2.2 | 2.3 | 2.6 | 2.3 |
| EyeEar | 1.9 | 2.4 | 3.0 | 2.5 |
| SnEye | 3.1 | 3.4 | 4.0 | 3.9 |
| NarEye | 2.3 | 2.4 | 2.7 | 2.7 |
| Interorb | 2.7 | 2.7 | 3.3 | 3.0 |
| EarL | 0.8 | 1.1 | 0.9 | 1.0 |
| Internar | 0.8 | 1.0 | 1.0 | 0.9 |

Table 5. Mensural data for the adult types of Pachydactylus melachlani, sp. nov. Abbreviations as in Materials and methods. All measurements in mm.

|  | NMNW R | NMNW R NMNW R | CAS | CAS | CAS | CAS | CM | TM |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 10499 | 10496 | 10498 | 125850 | 125852 | 125853 | 186293 | 119309 | 54735 |
|  | holotype | paratype | paratype | paratype | paratype | paratype | paratype | paratype | paratype |
| Sex | male | female | male | female | female | male | female | female | female |
| SVL | 43.0 | 48.7 | 48.1 | 40.4 | 37.8 | 41.0 | 46.0 | 44.3 | 38.4 |
| ForeaL | 6.7 | 7.5 | 6.7 | 5.2 | 5.2 | 5.6 | 5.9 | 5.9 | 5.4 |
| CrusL | 7.2 | 9.0 | 8.1 | 6.6 | 6.1 | 6.4 | 6.8 | 6.8 | 6.3 |
| TailL | 47.1 | 48.7 | 4.8 | 45.1 | 38.8 | 32.4 | 2.4 | 41.6 | 22.1 |
| $\quad$ (regen.) | N/A | 22.3 | broken | 24.9 | N/A | 31.2 | broken | 24.0 | 2.4 |
| TailW | 4.1 | 3.5 | 4.3 | 4.6 | 4.0 | 5.3 | N/A | 4.4 | 2.6 |
| TrunkL | 16.9 | 21.5 | 22.5 | 16.4 | 15.9 | 17.2 | 19.2 | 19.6 | 15.3 |
| HeadL | 13.0 | 14.0 | 13.7 | 11.9 | 11.5 | 11.6 | 13.1 | 12.5 | 12.1 |
| HeadW | 9.0 | 8.9 | 9.6 | 8.1 | 7.6 | 7.8 | 9.7 | 8.6 | 6.9 |
| HeadH | 4.7 | 5.6 | 5.5 | 4.0 | 4.1 | 4.0 | 4.8 | 4.9 | 4.0 |
| OrbD | 3.4 | 3.8 | 3.5 | 3.0 | 2.7 | 2.7 | 3.2 | 2.8 | 3.4 |
| EyeEar | 3.4 | 3.1 | 3.9 | 2.8 | 2.9 | 2.8 | 3.4 | 3.5 | 3.0 |
| SnEye | 4.7 | 5.5 | 5.2 | 4.5 | 4.2 | 4.4 | 5.0 | 4.5 | 4.6 |
| NarEye | 3.3 | 3.8 | 3.8 | 3.2 | 3.1 | 3.2 | 4.0 | 3.6 | 3.2 |
| Interorb | 3.5 | 3.5 | 4.0 | 3.2 | 3.0 | 3.1 | 3.4 | 3.5 | 2.7 |
| EarL | 1.4 | 1.3 | 0.8 | 0.9 | 0.7 | 0.8 | 1.4 | 0.8 | 0.8 |
| Internar | 1.2 | 1.3 | 1.4 | 1.1 | 1.0 | 1.3 | 1.4 | 1.4 | 1.1 |

Table 6. Mensural data for the types of Pachydactylus carinatus, sp. nov. Abbreviations as in Materials and methods. All measurements in mm .

|  | CAS | CAS | CAS | CAS | CAS | CAS | PEM | TM | TM | TM |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 201908 | 186340 | 201910 | 201913 | 203501 | 203502 | 11966 | 27949 | 34204 | 81098 |
|  | holotype | paratype | paratype | paratype | paratype | paratype | paratype | paratype | paratype | paratype |
| Sex | female | male | male | male | male | male | female | male | male | male |
| SVL | 45.7 | 42.0 | 44.0 | 42.5 | 42.5 | 41.4 | 43.5 | 37.2 | 39.6 | 40.7 |
| ForeaL | 6.2 | 6.2 | 6.2 | 5.6 | 6.0 | 6.2 | 5.9 | 5.7 | 5.9 | 6.3 |
| CrusL | 7.9 | 7.6 | 7.3 | 7.6 | 7.2 | 7.3 | 6.8 | 7.2 | 6.5 | 7.0 |
| TailL | 45.6 | 38.8 | 39.1 | 36.0 | 2.9 | 40.6 | 42.1 | 42.4 | 40.0 | 43.0 |
| (regen.) | 5.3 | 30.4 | 28.7 | 24.6 | broken | 5.2 | N/A | 22.3 | 1.6 | N/A |
| TailW | 3.6 | 4.3 | 4.3 | 3.8 | N/A | 4.4 | 4.3 | 3.2 | 3.5 | 3.5 |
| TrunkL | 20.2 | 15.4 | 17.6 | 18.3 | 15.7 | 17.9 | 18.8 | 16.3 | 16.4 | 15.7 |
| HeadL | 13.8 | 12.6 | 12.5 | 12.3 | 12.3 | 11.7 | 11.3 | 10.6 | 11.4 | 1.9 |
| HeadW | 8.4 | 8.0 | 7.5 | 7.4 | 8.1 | 8.3 | 8.5 | 7.8 | 8.4 | 7.6 |
| HeadH | 4.7 | 3.9 | 4.0 | 4.6 | 4.4 | 4.6 | 4.7 | 4.3 | 4.6 | 4.2 |
| OrbD | 3.4 | 3.0 | 3.0 | 2.8 | 3.1 | 2.9 | 2.9 | 2.6 | 3.0 | 3.1 |
| EyeEar | 3.1 | 2.5 | 3.1 | 3.2 | 3.0 | 3.5 | 3.1 | 2.9 | 2.9 | 3.1 |
| SnEye | 4.6 | 4.2 | 4.7 | 4.7 | 4.4 | 4.4 | 4.4 | 4.1 | 4.1 | 4.2 |
| NarEye | 3.4 | 3.1 | 3.1 | 3.3 | 3.3 | 3.0 | 3.2 | 3.1 | 3.1 | 3.1 |
| Interorb | 3.3 | 3.1 | 3.3 | 3.1 | 3.1 | 3.2 | 2.8 | 3.4 | 2.8 | 2.8 |
| EarL | 1.1 | 0.8 | 0.9 | 0.8 | 0.9 | 0.8 | 1.1 | 0.9 | 0.9 | 0.8 |
| Internar | 1.3 | 1.0 | 1.2 | 1.0 | 1.1 | 1.2 | 1.1 | 1.1 | 1.1 | 1.0 |

Table 7. Mensural data for the types of Pachydactylus visseri, sp. nov. Abbreviations as in Materials and methods. All measurements in mm.

|  | CAS | NMNW | TM | TM | TM | TM | TM | TM |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 201874 | R 8979 | 57399 | 35363 | 50110 | 28289 | 35456 | 35455 |
|  | holotype | paratype | paratype | paratype | paratype | paratype | paratype | paratype |
| Sex | male | male | female | male | male | male | female | female |
| SVL | 38.6 | 46.0 | 42.4 | 43.5 | 38.3 | 43.5 | 36.8 | 38.9 |
| ForeaL | 5.8 | 6.1 | 6.6 | 6.1 | 4.1 | 6.5 | 5.4 | 5.4 |
| CrusL | 7.0 | 7.1 | 7.0 | 7.4 | 6.9 | 7.3 | 6.4 | 6.3 |
| TailL | 3.0 | 47.3 | 38.4 | 3.0 | 41.0 | 44.8 | 41.1 | 46.7 |
| $\quad$ (regen.) | broken | N/A | broken | broken | N/A | 13.0 | N/A | N/A |
| TailW | N/A | 3.6 | 2.7 | N/A | 2.5 | 4.4 | 2.4 | 3.7 |
| TrunkL | 17.2 | 17.4 | 19.1 | 17.1 | 16.2 | 18.9 | 14.8 | 16.8 |
| HeadL | 12.3 | 13.3 | 13.3 | 12.0 | 10.6 | 12.4 | 10.1 | 10.9 |
| HeadW | 7.3 | 7.6 | 7.5 | 8.3 | 6.7 | 8.4 | 7.1 | 7.7 |
| HeadH | 4.4 | 4.2 | 4.7 | 5.1 | 3.6 | 5.4 | 4.7 | 5.3 |
| OrbD | 3.0 | 3.1 | 3.8 | 3.5 | 3.0 | 3.2 | 3.1 | 3.2 |
| EyeEar | 3.1 | 3.6 | 2.7 | 3.6 | 2.9 | 3.8 | 3.0 | 3.1 |
| SnEye | 4.1 | 4.3 | 5.6 | 4.2 | 3.9 | 4.6 | 3.8 | 4.4 |
| NarEye | 3.2 | 2.9 | 3.7 | 3.3 | 3.1 | 3.3 | 2.9 | 3.2 |
| Interorb | 2.5 | 3.3 | 3.3 | 3.6 | 3.1 | 3.6 | 2.7 | 3.4 |
| EarL | 0.8 | 1.0 | 1.1 | 0.9 | 0.8 | 0.8 | 0.6 | 0.8 |
| Internar | 1.1 | 1.2 | 1.8 | 1.5 | 1.0 | 1.2 | 1.2 | 1.1 |

Table 8. Mensural data for the adult types of Pachydactylus goodi, sp, nov. See Variation section for information regarding juvenile paratype. Abbreviations as in Materials and methods. All measurements in mm.

|  | TM 27962 holotype | $\text { TM } 84505$ paratype | $\begin{gathered} \text { CAS } 231878 \\ \text { paratype } \end{gathered}$ |  | $\begin{gathered} \text { TM } 45097 \\ \text { holotype } \end{gathered}$ | $\begin{gathered} \text { TM } 85000 \\ \text { paratype } \end{gathered}$ | $\begin{gathered} \text { TM } 85002 \\ \text { paratype } \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sex | male | female | male | Sex | male | male | juvenile |
| SVL | 50.0 | 45.5 | 41.4 | SVL | 39.4 | 42.9 | 27.3 |
| ForeaL | 7.2 | 6.9 | 5.6 | ForeaL | 5.6 | 6.7 | 4.1 |
| CrusL | 8.8 | 8.8 | 5.9 | CrusL | 6.6 | 7.8 | 4.4 |
| TailL | 55.8 | 2.5 | 47.0 | TailL | 40.1 | 35.2 | 3.8 |
| (regen.) | 37.3 | broken | N.A | (regen.) | 3.9 | tip cut | broken |
| TailW | 3.6 | N/A | 3.8 | TailW | 5.4 | 6.6 | 2.3 |
| TrunkL | 20.3 | 18.6 | 18.6 | TrunkL | 15.7 | 17.1 | 10.8 |
| HeadL | 14.0 | 13.7 | 11.5 | HeadL | 12.0 | 12.6 | 8.5 |
| HeadW | 9.9 | 8.0 | 8.1 | HeadW | 7.8 | 9.2 | 6.1 |
| HeadH | 5.8 | 4.9 | 4.8 | HeadH | 5.0 | 6.1 | 3.8 |
| OrbD | 3.8 | 3.4 | 3.2 | OrbD | 3.1 | 3.2 | 2.4 |
| EyeEar | 4.3 | 3.6 | 3.3 | EyeEar | 3.5 | 4.0 | 2.5 |
| SnEye | 5.6 | 4.8 | 4.7 | SnEye | 4.6 | 5.1 | 4.0 |
| NarEye | 4.0 | 3.4 | 3.3 | NarEye | 3.2 | 3.9 | 2.6 |
| Interorb | 4.0 | 3.3 | 3.2 | Interorb | 3.2 | 4.3 | 2.7 |
| EarL | 1.2 | 1.0 | 1.0 | EarL | 0.9 | 0.9 | 0.4 |
| Internar | 1.5 | 1.5 | 1.3 | Internar | 1.5 | 1.5 | 0.9 |

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# Three Additional New Species of Aristochroa Tschitschérine (Coleoptera: Carabidae: Pterostichini) from the Gaoligongshan of Western Yunnan Province, China 

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#### Abstract

Three new species of the genus Aristochroa Tschitschérine are described from the Gaoligongshan of western Yunnan Province, China: A. yuae Kavanaugh and Liang, sp. nov. (type locality $=10.1$ to 11.5 km west of Shibali, $\mathbf{3 2 2 5} \mathrm{m}$, Fugong County); $\boldsymbol{A}$. exochopleurae Kavanaugh and Liang, sp. nov. (type locality = Fengxue Yakou, 3290 m , Lushui County); and A. splendida Kavanaugh and Liang, sp. nov. (type locality = second cirque south of Shibali Yakou, 3780 m , Fugong County). Members of these new species are distinguished from each other and from all previously described Aristochroa species on the basis of features of pronotal and elytral shape and chaetotaxy, apical abdominal chaetotaxy, body color and development of microsculpture, and form of both male and female genitalia. Critical morphological features, habitat, and geographical distribution are illustrated for each species.


Aristochroa Tschitschérine, 1898, is one of the genera included in the carabid beetle tribe Pterostichini. To date, 26 species of this genus have been described from Yunnan, Sichuan, Xizang (Tibet), Qinghai, and Gansu Provinces in China (Tschitschérine 1898, 1903; Straneo 1938; Xie and Yu 1993; Sciaky and Wrase 1997; Zamotajlov and Fedorenko 2000; Liang and Yu 2002; Tian 2004), including one species from Gaoligongshan of western Yunnan (Kavanaugh and Liang, 2003). One additional species, A. watanabei Ito and Imura (2005), has been described from northeastern Myanmar (Burma), the first record for this genus outside of China. Nearly half (13) of these 27 known Aristochroa species were discovered in just the past decade, as more remote montane areas of China and Myanmar have been opened to both tourism and biotic inventory work; and additional new species can be anticipated as previously unstudied areas in this region are sampled.

Since July, 2000, when we collected the first specimens of Aristochroa abrupta Kavanaugh and Liang (Kavanaugh and Liang 2003), our continued fieldwork toward an inventory of the carabid beetle species of the Gaoligong Mountains (Gaoligongshan) has produced an additional 80 Aristochroa specimens from that area. Our attempts to identify these new specimens included (1) using the available keys to species (Xie and Yu 1993; and Liang and Yu 2002); (2) comparing features of our new specimens with those of identified material available at the Institute of Zoology (Beijing); and, (3) comparing character state information provided in the original and subsequent descriptions of all species not included in the keys or represented by available, identified material with the features of the new specimens in hand. Our morphological and distributional comparisons of these specimens with representatives and/or descriptions of all known species have convinced us that they represent three additional species unknown to science. The purpose of this paper is to
describe these new species and to identify those features which distinguish their adults from each other and from all other known species. Because additional species are very likely to be discovered soon in other parts of China, and perhaps also in other, adjacent countries, we refrain from providing here yet another key that is likely to become obsolete very soon.

## Materials and Methods

This study is based on the examination of 102 specimens of Aristochroa species collected during our fieldwork in the Gaoligongshan in 2000 through 2005 and additional material representing other congeneric species deposited in the collection of the Institute of Zoology in Beijing. Codens for collections cited in this paper are as follows:

$$
\begin{array}{ll}
\text { CAS } & \text { California Academy of Sciences, San Francisco, California 94103, U.S.A. } \\
\text { IOZ } & \text { Institute of Zoology, Chinese Academy of Sciences, Beijing 100080, China } \\
\text { KIZ } & \text { Kunming Institute of Zoology, Kunming, Yunnan Province, China }
\end{array}
$$

We also have relied heavily on species descriptions and illustrations presented in the papers listed in our References section for comparisons of the characteristics of our three new species with those of all previously described species. This is due in part to the fact that we have been unable to study the type specimens of many of the recently described species, and in part because the descriptions and their accompanying illustrations are of sufficient quality and detail to permit meaningful comparisons. As part of the descriptive format for each of the new species described in this paper, we present a section entitled "Comparisons with other species". In these sections, we first distinguish adults of our new species from those of the 14 species included in the Liang and Yu's (2002) key to species by citing the final couplet to which specimens of the new species run in that key. We then cite features that distinguish members of our new species from the other species that run to that same couplet. Species represented in the key include: Aristochroa balangensis Xie and Yu (1993), A. casta Tschitschérine (1898), A. deqinensis Xie and Yu (1993), A. deuvi Xie and Yu (1993), A. freyi Straneo (1938), A. gratiosa Tschitschérine (1898). A. kaznakovi Tschitschérine (1903), A. latecostata (Fairmaire, 1887), A. militaris Sciaky and Wrase (1997), A. perelegans Tschitschérine (1898), A. venusta Tschitschérine (1898), A. venustoides Xie and Yu (1993), A. wangi Xie and Yu (1993), and A. Zhongdianensis Liang and Yu (2002).. Finally, we cite features that distinguish our new species from each other and from members of the 13 other species that are not included in Liang and Yu's key, namely: Aristochroa aba Tian (2004). A. abrupta Kavanaugh and Liang (2003), A. chuanxiensis Tian (2004). A. dimorpha Zamotajlov and Fedorenko (2000), A. kangdingensis Zamotajlov and Fedorenko (2000). A. Lama Tian (2004). A. lanpingensis Tian (2004), A. longiphallus Tian (2004). A. morvani Tian (2004). A. mosuo Tian (2004), A. panda Tian (2004), A. sciakyi Zamotajlov and Fedorenko (2000), and A. watanabei Ito and Imura (2005).

All measurements were made with the aid of an ocular micrometer in a Leitz stereoscopic dissecting microscope. Total body length $=$ the linear distance along the midline from the apex of longer mandible to the apex of longer elytron. Pronotal length $(\mathrm{PL})=$ the linear distance along the midline from the anterior margin to the posterior margin; and pronotal width (PW) = the linear distance across the widest part of the pronotum measured at $90^{\circ}$ to the longitudinal axis. Elytral length $(E L)=$ the linear distance along the midline from the apex of the scutellum to the apex of the longer elytron: and elytra width $(E W)=$ the linear distance at the widest point across both elytra measured at $90^{\circ}$ to the longitudinal axis. Ratios cited in descriptions (i.e., EL/PL, PW/PL, and EL/EW) are based on these measurements. Because the specific details of how measurements (e.g., total body length) were made is typically not included in the descriptions cited in the literature, we include
measurements and ratios here for descriptive purposes only, not for comparative purposes except among those species which we are describing.

Typically, one of the most attractive features of adults of Aristochroa species is their metallic reflection or "color" and, in most species, the appearance of contrasting colors on alternating intervals of the elytra. Virtually all previous descriptions of these species have included characters of dorsal coloration and we have used such characters in our descriptions here; but these descriptions of color are very difficult to interpret, especially on the elytra, for several reasons. First, factors that affect the color perceived include the depth of impression of microsculpture, convexity of the surface, especially of the elytral intervals, the angle at which one views the surface, and the angle at which the surface is illuminated for viewing. For example, the degree to which the color of elytral intervals $1,3,5$, and 7 contrasts with that of intervals $2,4,6$, and 8 changes in some species as one rotates a specimen from side to side while viewing it illuminated under a microscope. Second, maturity of a specimen (i.e., whether it is fully pigmented and sclerotized or slightly teneral) may influence both the intensity and hue of the metallic color perceived. Finally, based on the examination of longer series, we find that there is typically more individual variation in the metallic "color" of head, pronotum, and elytra within Aristochroa species than has been recorded in most descriptions. For all these reasons, we have relied as little as possible on the use of color characters in comparisons provided with our species descriptions, using them comparatively only where the differences are consistent and easily observed and mainly for descriptive purposes.

Visualization and study of female genitalic structures were enhanced by staining dissections with Chlorozol Black E. Digital color images of specimens and selected structures and dissections were captured using an Automontage ${ }^{\circledR}$ imaging system from Synchroscopy. Distribution maps were prepared using Arcview® software. Geographical coordinates provided here for localities were recorded with a Garmin 12 global positioning unit, using Datum WSG 84.

## Descriptions of New Species

## Aristochroa yuae Kavanaugh and Liang, sp. nov.

Figures 1, 4B, 5B, 6B, 7B, 8B, 9, 12A and C.
Types.- Holotype: a male, deposited in IOZ, labeled, "CASENT 1017110" / "China, Yunnan
 E098.71354 ${ }^{\circ}$ to N27.20676${ }^{\circ}$ E098.71763"" / "3225-3290 m, 8 May 2004, Stop \#DHK-2004-041, D.H. Kavanaugh, C. E. Griswold, Liang H.-B., Li X.-Y., \& Zhu B.-X. collectors"/ "Holotype Aristochroa yuae Kavanaugh \& Liang sp. nov. des. by D. H. Kavanaugh 2006" [red-edged label]. A total of 25 paratypes ( 13 males and 12 females) are deposited in CAS, IOZ, and KIZ (see specimen data below, under Geographic distribution).

Type locality.- 10 to 11.5 km west of Shibali, 3225-3290 m, Lishadi Township, Fugong County, Yunnan Province, China.

Diagnosis.- Adults of A. yuae are distinguished from all other known species by the following combination of character states dorsal surface (Fig. 1) with distinct coppery metallic reflection with greenish highlights; eyes large and convex; glossal sclerite with three pairs of apical setae; pronotum (Fig. 4B) moderately wide (ratio PW/PL $=1.27$ to 1.41 ) and moderately narrowed basally, lateral margin shallowly and gradually sinuate in posterior one-fourth, hind angles slightly obtuse, two marginal pronotal setae at/near and anterior to the middle in most individuals (one or three or four seen unilaterally in a few specimens), basal foveae smooth, impunctate; proepisternum smooth, impunctate; elytra with subapical sinuation lateral margin (Fig. 5B) moderately deep, apex of elytral epipleuron roundly and slightly abruptly tapered to merger with elytral lateral margin, ely-
tral microsculpture deeply and approximately equally impressed on all intervals, intervals 1 , $3,5,7$, and 8 moderately and distinctly convex, interval 3 with two setae in most individuals (one or three setae unilaterally in a few specimens); sternum VII of males with two pairs of apical paramedial setae; males with median lobe of aedeagus slightly long and thin, midshaft tubular, without ventral swelling just basal to midshaft bend, preapical shaft slightly bent dorsally basal to apical lamella, apical lamella very long, curved ventrally nearly $90^{\circ}$ relative to preapical shaft in lateral aspect (Fig. 6B), narrowly subtriangular, bluntly pointed, and markedly deflected right in ventral aspect (Fig. 6 E ); females with hemisternites of sternum VIII (Fig. 7B) with deeply incised membranous areas medially, spermathecal gland long and slightly swollen at anterior end (Fig. 8B).

Comparisons with other species.Using the key of Liang and Yu (2002), specimens of this species run to couplet 13 , along with specimens of $A$. gratiosa and $A$. militaris. They can be distinguished from specimens of $A$. gratiosa and/or A. militaris by their more distinctly coppery dorsal metallic reflection with greenish highlights (more distinctly greenish with coppery highlights in A. gratiosa, dark bronze dorsal metallic reflection in A. militaris); pronotum (Fig. 4B) relatively broader


Figltre 1. Digital photograph of holotype of Aristochroa yuae sp. nov., dorsal aspect; scale line $=1.0 \mathrm{~mm}$.
(ratio $\mathrm{PW} / \mathrm{PL}=1.27$ to 1.41 , compared with 1.20 to 1.25 in A. gratiosa). only two marginal pronotal setae at/near and anterior to the middle in most individuals (three to five such setae in A. gratiosa and three such setae in A. militaris); subapical sinuation of the elytra (Fig. 5B) moderately deep (very shallow in A. gratiosa); microsculpture of elytral intervals 1.3.5. and 7 deeply impressed (only faintly visible in A. militaris); and, in males, sternum VII with two pairs of apical paramedial setae (only one pair of such setae in A. militaris). the median lobe of the aedeagus (Fig. 6B and E) slightly longer and thinner (shorter and thicker in A. gratiosa) with the midshaft tubular (distinctly broadened toward apex in A. gratiosa) and without a ventral swelling just basal to the midshaft bend (present in A. militaris), the preapical shaft slightly bent dorsally basal to apical lamella (straight in A. gratiosa and A. militaris), and the apical lamella very long, curved ventrally nearly $90^{\circ}$ relative to preapical shaft in lateral aspect (apical lamella moderate in length and straight relative to preapical shaft in lateral aspect in A . grafiosa. slightly curved ventrally in A. militaris). and narrowly subtriangular, bluntly pointed apically: and markedly deflected right in ventral aspect (apical lamella broadly subtriangular, apically rounded and nearly symmetrical in ventral aspect in A. gratiosa. broadly triangular, broadly pointed apically, and slightly deflected right in A. militaris).

Adults of A. yuae (Fig. 4B) are easily distinguished from those of A. abrupta (Fig. 4A) by their
relatively shorter and broader pronotum, only shallowly and gradually sinuate pronotal lateral margins (deeply and abruptly sinuate in A. abrupta), presence of only two marginal pronotal setae at/near and anterior to the middle in most individuals (three to five such setae in A. abrupta), and numerous differences in the median lobe of the genitalia of males (compare Figs. 6B and E with Figs. 6A and D). Aristochroa yuae adults are distinguished most easily from those of Aristochroa exochopleurae sp. nov. by the roundly and slightly abruptly tapered apex of the elytral epipleuron (Fig. 5B) compared with the angulate to denticulate elytral epipleural apex in A. exochopleurae (Fig. 5C), as well as by several differences in the median lobe of the genitalia of males (compare Figs. 6B and E with Figs. 6C and F) and the length and shape of the spermathecal gland in females (compare Fig. 8B with Fig. 8C). Based on the limited data available at present for Aristochroa splendida sp. nov., it appears that A. yuae adults can be distinguished from those of $A$. splendida by their larger and more convex eyes (Fig. 1) (slightly smaller and flatter in A. splendida, Fig. 3), pronota (Fig. 4B) relatively longer (ratio PW/PL $=1.27$ to $1.41 ; 1.50$ in A. splendida) and more narrowed basally (compare with Fig. 4D for A. splendida), with lateral margin shallowly and gradually sinuate (bisinuate in A. splendida), only two marginal pronotal setae at/near and anterior to the middle in most individuals (three such setae in A. splendida), elytral intervals $1,3,5$, and 7 with deeply impressed microsculpture (microsculpture barely visible on these intervals in A. splendida), and in females, with the hemisternites of sternum VIII (Fig. 7B) with deeply incised membranous areas medially (entire, without membranous areas in A. splendida, Fig. 7D), and the spermathecal gland (Fig. 8B) long (shorter in A. splendida, Fig. 8D).

From adults of the remaining species, those of $A$. yuae can be distinguished as follows: $A$. $a b a$, A. morvani, and A. mosuo adults have their proepisterna distinctly punctate (impunctate in A. yuae); A. lanpingensis adults have the lateral pronotal margin deeply and abruptly sinuate anterior to acute hind angle and those of A. chuanxiensis lack any trace of sinuation posteriorly on the lateral pronotal margin and the hind angles are distinctly obtuse (lateral pronotal margin shallowly and gradually sinuate and hind angles slight obtuse in A. yuae); adults of $A$. watanabei have 2 pairs of apical setae on the glossal sclerite (three such pairs in A. yuae); adults of A. watanabei and A. lama have three and those of A. panda have four marginal pronotal setae at/near and anterior to the middle (only two such setae in most A. yuae; all of the few individuals seen with more than two setae had these unilaterally only); A. longiphallus adults have the dorsal metallic reflection coppery with distinct bluish highlights, pronotum with lateral margin deeply and densely crenulate and hind angles rectangular (coppery dorsal metallic reflection with greenish highlights, pronotum with lateral margin shallowly and sparsely or densely crenulate and hind angles slightly obtuse in A. yuae); adults of A. kangdingensis have the microsculpture of elytral intervals $1,3,5$, and 7 effaced (deeply impressed on these intervals in A. yuae); elytral intervals $1,3,5$, and 7 are only slightly convex and intervals $2,4,6$, and 8 are flat in adults of A. dimorpha and the odd intervals are markedly convex and the even intervals flat or slightly convex in A. sciakyi (odd intervals moderately convex and even intervals slightly convex in A. yuae. Males of A. yuae are easily recognizable among all described species on the basis of the shape of the median lobe of the aedeagus alone (compare Figs. 6B and E with illustrations for A. abrupta (Figs. 6A and D), A. exochopleurae (Figs. 6C and F) and those for other species described in papers cited in the References section); however, too few descriptions and illustrations of female genitalia have been published to make this claim for females..

Description.- Total length males 11.4 to 14.7 mm , females 12.9 to 14.8 mm ; ratio EL/PL in males 2.57 to 2.72 (mean $=2.64$ ), in females EL/PL 2.53 to 2.69 (mean $=2.62$ ). Head, pronotum, and elytra black or piceous, venter black, tibiae black or piceous; dorsal surface with marked coppery metallic reflection (with greenish highlights in most individuals) (Fig. 1); elytral intervals
either all concolorous coppery or intervals $1,3,5$, and 7 dark coppery or black contrasting with intervals $2,4,6$ and 8 greenish-coppery or coppery.

Head. Eyes convex, large, diameter at least twice length of angulate tempora. Frons densely and very finely punctulate; frontal furrows moderately long and deep, slightly divergent posteriorly and terminated posteriorly as two or more short, sharply-defined parallel furrows separated by convexities, furrows slightly to markedly rugose, impunctate. Vertex smooth or slightly rugose, microsculpture comprised of very shallowly impressed, indistinct transverse meshes. Two pairs of supraorbital setae present. Glossal sclerite with three pairs (six) of apical setae (lateral short seta on one or both sides broken and missing in some specimens).

Thorax. Pronotum (Fig. 4B) slightly short and moderately broad, ratio PW/PL $=1.27$ to 1.41 (mean $=1.34$ ), greatest width distinctly anterior to middle; lateral margin smoothly arcuate from apical angles to one-fourth from base, then slightly and gradually sinuate to hind angles, with shallow and sparse to dense crenulations present along entire margin; hind angles slightly obtuse; lateral margin with two setae near and/or anterior to middle in most individuals (with only one or with three or four setae in a few individuals); pronotal disc with few to many finely etched transverse wrinkles, otherwise smooth or with sparse and indistinct punctulae only, microsculpture comprised of shallowly impressed, distinctly transverse meshes; basal foveae moderately deep, with two longitudinal sulci present; area between sulci flat or slightly convex, smooth, impunctate, broad anteriorly, distinctly narrowed posteriorly by convergence of sulci; inner sulcus about 1.5 to 2.0 times as long as outer sulcus, slightly to distinctly deflected laterally near base, smooth and impunctate; outer sulcus slightly curved (anterior and posterior ends slightly deflected medially), slightly sigmoid (anterior end of sulcus slightly deflected laterally and posterior end slightly deflected medially), or straight or nearly so, smooth and impunctate; laterobasal ridge (external to outer sulcus) narrow to moderate in width. Prosternum with median longitudinal impression present, faint, transverse groove anterior to coxae absent or present as vague, disrupted depression. Proepisternum, mesepisternum, and metepisternum impunctate. Elytra more or less symmetrically subovoid or subovoid and distinctly narrowed basally, relatively shorter and wider in females than males, ratio EL/EW in males $=1.44$ to $1.58($ mean $=1.51)$, in females 1.39 to 1.48 (mean $=1.44)$, widest slightly (in males) or distinctly (in females) posterior to middle; subapical sinuation deep; elytral epipleuron roundly but slightly abruptly tapered posteriorly to merger with lateral elytral margin (Fig. 5B); elytral microsculpture comprised of isodiametric meshes, deeply and more or less equally impressed on all intervals; basal margination slightly concave anteriorly, slightly wavy, basal and lateral marginations joined at distinct obtuse angle at humerus; humeral tuberosity absent; striae deeply impressed. very slightly punctate: elytral intervals $1,3,5,7$. and 8 moderately convex. intervals 2, 4, and 6 only slightly convex: intervals 4 and 6 entire. without catenations; intervals 1, 3, 5, and 7 distinctly broader than intervals 2.4 .6 . and 8 .. width of interval 3 at middle 1.5 to 2.3 (mean $=1.9$ ) times width of interval 4: interval 3 with two setae, one each in basal and apical one-thirds (only one or three setae present unilaterally in a very few individuals); interval 5 merged with interval 7 at or near level of subapical sinuation; intervals 4,5 , and 6 not fused posteriorly.

Abdomen. Sternum VII with two pairs of apical paramedial setae in both males and females (only one seta seen unilaterally in very few male specimens). Aedeagus of male genitalia with median lobe (Fig. 6B and E) long and moderately broad: in lateral aspect (Fig. 6B), bend of shaft subangulate and distinctly less than $90^{\circ}$. ventral sub-basal swelling present and slightly developed, ventral basomedial and subapical swellings absent, midshaft more or less tubular, consistent in diameter: preapical shaft slightly bent dorsally before apical lamella. with shorter, more abrupt taper toward apex: preapical shaft abruptly widened and markedly bulged left subapically in ventral aspect (Fig. 6E): apical lamella very long, curved ventrally nearly $90^{\circ}$ relative to preapical shaft (in
lateral aspect. Fig. 6B), narrowly subtriangular, apically pointed, and markedly deflected right in ventral aspect (Fig. 6E); thorn-shaped sclerite of internal sac (see Ito and Imura, 2005) not visible in cleared specimens, apparently absent). Female genitalia with hemisternites of sternum VIII with deeply incised membranous area medially (Fig. 7B); gonostylus (stylomere II) of ovipositor broad, arcuate; spermatheca pointed and slightly coiled on anterior end; spermathecal gland long, at least 1.5 times as long as spermatheca, tubular and distinctly swollen at anterior end (Fig. 8B).

Sexual dimorphism. - The elytra are relatively wider in females than in males (means values for the ratio EL/EW $=1.44$ in females and 1.51 in males) and the greatest elytral width is more distinctly posterior to middle in females than in males.

Geographical distribution.- Fig. 12A and C. At present known only from eastern slope of the Gaoligongshan in the drainage system of the north fork of Yamu He (Yamu River) in Lishadi Township, Fugong County, Yunnan Province, China. We have examined a total of 24 specimens (including the holotype and 23 paratypes) from the following localities: " 12 km above Shibali on Shibali Road, N27.19980º $0098.71375^{\circ "}$ / " 3200 m , 5 May 2004, Stop \#LHB-2004-022, Liang H.-B., Li X.Y., \& Xie M. collectors" ( 2 males); "11.5 km above Shibali on Shibali Road, N27.20676º/E098.71763*" / " 3290 m, 6 May 2004, Stop \#DHK-2004-036, D.H. Kavanaugh, C. E. Griswold, Liang H.-B., \& Zhu B.-X. collectors" ( 1 female); "10.1 km above Shibali on Shibali Road, N27.20049 , E98.71354"" / "3225 m, 6 May 2004, Stop \#DHK-2004-037, D.H. Kavanaugh, C. E. Griswold, Liang H.-B., \& Zhu B.-X. collectors " (3 males and 1 female); "11.5 km above Shibali on Shibali Road, N27.20676º098.71763"" / "3290 m, 8 May 2004, Stop \#DHK-2004-040, D.H. Kavanaugh, C. E. Griswold, Liang H.-B., Li X.-Y., \& Zhu B.-X. collectors" (1 male and 1 female); " 10.1 to 11.5 km above Shibali on Shibali Road, N27.20049 $/ \mathrm{E} 098.71354^{\circ}$ to N27.20676/E098.71763*" / "3225-3290 m, 8 May 2004, Stop \#DHK-2004-041, D.H. Kavanaugh, C. E. Griswold, Liang H.-B., Li X.-Y., \& Zhu B.-X. collectors" ( 2 male and 3 females); " 8.5 km above Shibali on Shibali Road, north fork of Yamu He, N27.18416/E098.72026"" / "3100 m, 9 May 2004, Stop \#DHK-2004042, D.H. Kavanaugh \& Liang H.-B. collectors" (1 male); "10 . 0 km W of Shibali on Shibali Road, 3221 m , N27.20055/E098.71399," / "5-16 August 2005, pitfall traps, Stop \#DHK-2005-061, D.H. Kavanaugh, P. Paquin, \& H.B. Liang collectors" ( 3 females); " 10.0 km W of Shibali on Shibali Road, 3200 m , N27.19980 /E098.71375"," / "5-6 August 2005, Stop \#DHK-2005-062, D.H. Kavanaugh, P. Paquin, H.B. Liang, \& D.Z. Dong collectors" ( 1 male); " 9.5 to 10.0 km W of Shibali on Shibali Road,
 2005-078, D.H. Kavanaugh, H.B. Liang, \& D.Z. Dong collectors" ( 2 males and 1 female); " 8.4 to 9.5 km W of Shibali on Shibali Road, N27.18770/E098.71936 ${ }^{\circ}$ to N27.19438。" / "E098.71486 ${ }^{\circ}$, 3160-3195 m, 16 August 2005, Stop\# DHK-2005-091, H. B. Liang collector" ( 1 female); " 4.0 km W of Shibali on Shibali Road,
 male); "10.0 km W of Shibali on Shibali Road, 3200 m ," / "N27.19980 $/$ E098.71375", 16 August 2005, Stop \#LHB-05-056, J. F. Zhang collector" (1 male and 1 female).

Geographical relations with congeners.- The known geographical range of $A$. yuae is distinctly allopatric with respect to all other known species of Aristochroa except A. splendida sp. nov. (Fig. 12 C). To date, all records for A. yuae are restricted to elevations between 2800 and 3300 meters on the eastern slope of the Gaoligongshan, whereas the single record for A. splendida is from 3710 m , on the ridge crest of the range, immediately above the drainage system (Yamu river system) in which A. yuae appears to be restricted. Additional sampling is needed to determine if these two species occur together at intermediate elevations here or elsewhere. The nearest known localities for A. abrupta and A. exochopleurae are about 46 kilometers north and 132 kilometers south, respectively, of the known range of $A$. yuae.

Geographical variation.- No locality-specific differences have been observed among individuals from the different localities sampled for this species.

Habitat distribution.- Specimens of A. yuae were found mainly along the road cut (Fig. 9A), between 4 and 11 kilometers west of Shibali, over an elevational range from 2800 to 3290
meters. During daytime hours, a few beetles were found under large ( 30 to 60 cm in diameter) stones at the base of the road cut (uphill side of the road). Many more were found at night, with the aid of headlamps, while they were actively walking on the bare soil of the roadcut base or wall or on leaf litter under overhanging vegetation. Vegetation in the area consisted mainly of bamboo and Rhododendron thickets, so dense as to form a virtually continuous cover, one to three meters tall, except along the roadcut itself and in adjacent disturbed areas, and a discontinuous overstory of mixed conifer (Tsuga sp.) and broadleaf deciduous (Acer, Litsea, and Sorbus spp.) trees. Beetles were also collected in pitfall traps on a gentle, southeast-facing slope (Fig. 9B), 10 to 50 meters north of and above the roadcut in an area of Rhododendron and bamboo thickets and sparsely scattered Tsuga sp.

Etymology.- This species epithet, a feminine genitive singular noun in apposition, is the Latinized surname of Professor Peiyu Yu of the Institute of Zoology, Chinese Academy of Sciences, Beijing, selected in recognition of her extensive experience with the genus Aristochroa and her continued helpful advice over the course of our projects in the Gaoligongshan and elsewhere in China.

## Aristochroa exochopleurae Kavanaugh and Liang, sp. nov. <br> Figures 2, 4C, 5C, 6C, 7C, 8C, 10, 12A and D.

Types.- Holotype: a male, deposited in IOZ, labeled, "CASENT 1017597" / "China, Yunnan, Lushui County, Luzhang Township, Pianma Road at Fengxue Yakou, N25.972283$/ E 098.68336^{\circ}$ ", $3150 \mathrm{~m}, 11$ May 2005," / "Stop\# 2005-007, D.H. Kavanaugh, H.B. Liang, C.E. Griswold, D.Z. Dong \& K.J. Guo collectors"/ "Holotype Aristochroa exochopleurae Kavanaugh \& Liang sp. nov. des. by D. H. Kavanaugh 2006" [rededged label]. A total of 54 paratypes ( 36 males and 18 females) are deposited in CAS, IOZ, and KIZ (see specimen data below, under Geographic distribution).

Type locality.- Pianma Road at Fengxue Yakou (pass), 3150 m , Luzhang Township, Lushui County, Yunnan Province, China.

Diagnosis.- Adults of both sexes of A. exochopleurae are distinguished from those of all other known species by the markedly projecting angulate to denticulate apices of their elytral epipleura (Fig. 5C).

Comparisons with other species.- Using the key of Liang and Yu (2002), specimens of this species run to couplet 13. with specimens of A. gratiosa Tschitschérine and A. militaris Sciaky and Wrase. However, they are easily distinguished from members of these two species, as well as from those of all other known species. by the markedly projecting angulate to denticulate apices of their elytral epipleura (Fig. 5C). Males of A. exochopletrrae also are easily recognizable among all described species on the basis of the shape of the median lobe of the aedeagus (compare Figs. 6C and F with illustrations for A. abrupta (Figs. 6A and D). A. yuae (Figs. 6B and E) and those for other species described in papers cited in the References section); however, too few descriptions and illustrations of female genitalia have been published to make this claim for females. Additional features that distinguish adults of A. exochopleurae from those of other species in which males have somewhat similar genitalia (namely. A. yuae. A. abrupta, A. watanabei, A. mosuo, and A. lanpingensis) include the following: pronotum with shallowly and gradually sinute lateral margins anterior to rectangular or slightly obtuse hind angles (deeply and abruptly sinuate lateral margins anterior to distinctly acute hind angles in A. lanpingensis adults and to rectangular hind angles in $A$. abrupta adults): thoracic episterna smooth (episterna distinctly punctate in A. mosuo adults); and sternum VIII of males with a single pair of apical paramedial setae (two pairs of such setae in A. yuae and $A$. watanabei males).

Description- Total length males 12.9 to 15.6 mm , females 13.9 to 15.3 mm ; ratio EL/PL in males 2.48 to 2.73 (mean $=2.59$ ). in females EL/PL 2.47 to 2.72 (mean $=2.59$ ). Head, pronotum,
and elytra black or piceous, venter black, tibiae black or piceous; dorsal surface with marked greenish metallic reflection, with greenish highlights in most individuals (in some individuals, predominant color coppery with greenish highlights) (Fig. 2); elytral intervals either all concolorous coppery or intervals $1,3,5$, and 7 dark coppery or black contrasting with intervals 2,4 , 6 and 8 greenish-coppery or coppery.

Head. Eyes convex, large, diameter at least twice length of angulate tempora. Frons densely and very finely punctulate; frontal furrows long and very deep, slightly divergent posteriorly and terminated posteriorly as two or more short, sharply-defined parallel furrows separated by convexities, furrows slightly to markedly rugose, impunctate. Vertex smooth or slightly rugose, microsculpture comprised of very shallowly impressed, indistinct transverse meshes. Two pairs of supraorbital setae present. Glossal sclerite with two or three pairs of apical setae in approximately equal numbers of individuals (five setae also seen in some specimens).

Thorax. Pronotum (Fig. 4C) slightly longer, ratio $\mathrm{PW} / \mathrm{PL}=1.18$ to 1.37 (mean $=$ 1.27 ), greatest width distinctly anterior to middle; lateral margin smoothly arcuate from apical angles to one-fourth from base, then straight or very slightly and gradually sinuate to hind angles, with deep and dense crenulations present along entire margin; hind angles slightly obtuse or rectangular; lateral margin with two setae


Figure 2. Digital photograph of holotype of Aristochroa exochopleurae sp. nov., dorsal aspect; scale line $=1.0 \mathrm{~mm}$. near and/or anterior to middle in most individuals (with only one or with three setae in a few individuals); pronotal disc with few to many deeply etched transverse wrinkles, otherwise smooth or with sparse and indistinct punctulae only, microsculpture comprised of very shallowly impressed, distinctly transverse meshes barely visible in some areas; basal foveae very deep, with two longitudinal sulci present; area between sulci flat or slightly convex, smooth, impunctate, or finely and sparsely rugose, broad anteriorly, eliminated or nearly so posteriorly by convergence of sulci; inner sulcus about 1.5 to 2.0 times as long as outer sulcus, markedly deflected laterally near base, confluent with outer sulcus or nearly so near base, smooth and impunctate; outer sulcus slightly sigmoid (anterior end of sulcus slightly deflected laterally and posterior end slightly deflected medially) or straight or nearly so, smooth and impunctate; laterobasal ridge (external to outer sulcus) broad. Prosternum with median longitudinal impression absent or present and vague or distinct, transverse groove anterior to coxae absent or present as vague, disrupted depression. Proepisternum, mesepisternum, and metepisternum impunctate. Elytra more or less symmetrically subovoid or subovoid and distinctly narrowed basally, slightly shorter and wider in females than males, ratio EL/EW in males $=1.44$ to $1.60($ mean $=$
1.52 ), in females 1.34 to 1.50 (mean $=1.45$ ), widest at middle (in males) or slightly posterior to middle (in females); subapical sinuation deep; elytral epipleuron angulate or denticulate, abruptly truncate just anterior to merger with lateral elytral margin (Fig. 5C); elytral microsculpture comprised of isodiametric meshes, shallowly and more or less equally impressed on all intervals; basal margination slightly concave anteriorly, slightly wavy, basal and lateral marginations joined at distinct obtuse angle at humerus; humeral tuberosity absent; striae moderately impressed, very slightly punctate; elytral intervals $1,3,5,7$, and 8 moderately convex. intervals 2,4 , and 6 only slightly convex; intervals 4 and 6 entire, without catenations; intervals $1,3,5$, and 7 distinctly broader than intervals $2,4,6$, and 8 ., width of interval 3 at middle 2.0 to 2.5 (mean $=2.2$ ) times width of interval 4 ; interval 3 with two setae, one each in basal and apical one-thirds (only one or three setae present unilaterally in a very few individuals); interval 5 merged with interval 7 at or near level of subapical sinuation; intervals 4,5, and 6 not fused posteriorly.

Abdomen. Sternum VII with one pair of apical paramedial setae in males and two pairs in females (only one seta seen unilaterally in very few female specimens). Aedeagus of male genitalia with median lobe (Fig. 6C and F) moderate in length and width; in lateral aspect (Fig. 6C), bend of shaft evenly arcuate and less than $90^{\circ}$, ventral sub-basal swelling present and slightly developed, ventral basomedial and subapical swellings absent, midshaft more or less tubular, consistent in diameter, preapical shaft slightly bent dorsally before apical lamella, long, gradually tapered toward apex; preapical shaft not widened but slightly bulged right and left subapically in ventral aspect (Fig. 6F); apical lamella long, distinctly curved ventrally relative to preapical shaft (in lateral aspect, Fig. 6C), narrowly subtriangular, apically pointed, and slightly deflected right in ventral aspect (Fig. 6F); thorn-shaped sclerite of internal sac (see Ito and Imura, 2005) not visible in cleared specimens, apparently absent). Female genitalia with hemisternites of sternum VIII with deeply incised membranous area medially (Fig. 7C); gonostylus (stylomere II) of ovipositor broad, arcuate; spermatheca pointed and slightly coiled on anterior end; spermathecal gland long, at least 1.5 times as long as spermatheca, tubular, slightly swollen near anterior end and slightly narrowed at end (Fig. 8C).

Sexual dimorphism. - The elytra are relatively wider in females than in males (means values for the ratio EL/EW $=1.44$ in females and 1.52 in males) and the greatest elytral width is slightly posterior to middle in females and at middle in males. Males have a single pair of apical paramedial setae on sternum VII while females have two pairs of such setae.

Geographical distribution.- Fig. 12A and D. At present, known only from the crest of the Gaoligongshan at Fengxue Yakou (Pass) and within 0.5 km east and 0.6 west of that pass in Luzhang and Pianma Townships (respectively), Lushui County, Yunnan Province, China.). We have examined a total of 55 specimens (including the holotype and 54 paratypes) from the following localities: Luzhang Township: "Pianma Road at Fengxue Yakou, N25.972283 E098.68336", $3150 \mathrm{~m}, 11$ May 2005," / " Stop\# 2005-007. D.H. Kavanaugh. H.B. Liang. C.E. Griswold, D.Z. Dong \& K.J. Guo collectors" (1 male); "100 m S of Fengxue Yakou on E slope, N25.97195 $/ \mathrm{E} 098.68381^{\circ}$," " "3150 m, 11-21 May 2005. Stop\# 2005-008, pitfall trap. D.H. Kavanaugh. C.E. Griswold, \& K.J. Guo collectors: (3 males and 2 females): "Fengxue Yakou to 0.5 km E on Pianma Road, $3130-3150 \mathrm{~m}, \mathrm{~N} 25.97288^{\circ}$ E $098.68336^{\circ}$ to" / "N25.97347/E098.68780 , 17 May 2005, Stop\# 2005-013B, D.H. Kavanaugh, C.E. Griswold, H.B. Liang, D.Z. Dong. \& K.J. Guo collectors" (26 males and 16 females). Pianma Township: "Fengxue Yakou to 0.6 km W on Pianma Road, 3120-3150 m. N25.97288/E098.68336 ${ }^{\circ}$ to" / "N $25.97410^{\circ} / \mathrm{E} 098.67716^{\circ}$, 18 May 2005, Stop\# 2005-014. D.H. Kavanaugh. C.E. Griswold. H.B. Liang. D.Z. Dong. \& K.J. Guo collectors" ( 1 male); "Fengxue Yakou to 0.5 km W on Pianma Road, $3120-3150 \mathrm{~m}$, N $25.97288^{\circ} / \mathrm{E} 098.68336^{\circ}$ to" / "N25.97+10 $/$ E098.67716 . 19 May 2005. Stop\# 2005-016. D.H. Kavanaugh, C.E. Griswold, H.B. Liang, D.Z. Dong, \& K.J. Guo collectors" ( 6 males).

Geographical relations with congeners.- The known geographical range of a. exo-
chopleurae is distinctly allopatric with respect to all other known species of Aristochroa (Fig. 12 D). The nearest known locality for $A$. abrupta is about 183 kilometers north of the range of $A$. exochopleurae; and the nearest known localities for A. yuae and A. splendida are both about 132 kilometers north.

Geographical variation. - Unknown; known at present from a single area.
Habitat distribution.- Most specimens of A. exochopleurae were found along the road cut (Fig. 10B , both at the pass and across the steep slopes immediately east and west of it, at 3120 to 3150 meters elevation. During daytime hours, a few beetles were found under large ( 30 to 60 cm in diameter) stones at the base of the road cut (uphill side of the road). Many more were found at night, with the aid of headlamps, while they were actively walking on the bare soil of the roadcut base or wall or on leaf litter under overhanging vegetation. Vegetation in the area consisted mainly of bamboo and Rhododendron thickets, so dense as to form a virtually continuous cover, one to three meters tall, except along the roadcut itself and in rockslide areas. Beetles were also collected in pitfall traps on a steep, east-facing slope (Fig. 10A)., about 100 meters south of the pass on its eastern flank, in an area of taller (up to 5 meters high) Rhododendron and bamboo thicket.

Etymology.- This species epithet, a feminine genitive plural noun in appoisition, is a compound word derived from the Greek exochos, an adjective meaning jutting out, projecting, or prominent, and pleura, the Greek word for side, here referring specifically to the prominently projecting apices of the elytral epipleura seen in adult males and, to a slightly lesser extent, females of this species.

## Aristochroa splendida Kavanaugh and Liang, sp. nov.

Figures 3, 4D, 5D, 6D, 7D, 8D, 11, 12A and C.
Types.- Holotype: a female, deposited in IOZ, labeled, "CASENT 1017808" / "China, Yunnan, Fugong County, Lumadeng Township, second cirque S of Shibali Yakou at border post " 31 ", N27.20333º ${ }^{\circ}$ E098.69303"" / "3710 m, 17 August 2005, Stop\# DHK-2005-095, H.B. Liang, D.Z. Dong, \& J.F. Zhang collectors"/ "Holotype Aristochroa splendida Kavanaugh \& Liang sp. nov. des. by D. H. Kavanaugh 2006" [red-edged label].

Type locality.-Second cirque south of Shibali Yakou, 3710 m, Lu.... : s Township, Fugong County, Yunnan Province, China.

Diagnosis. - Females of A. splendida are distinguished from those of all other known species by the following combination of character states: head, pronotum, and elytra with brilliant green metallic reflection dorsally (Fig. 3), elytral intervals 1, 3, 5, and 7 distinctly convex with contrasting brilliant coppery metallic reflection and with nearly effaced microsculpture, at least at the interval centers; eyes slightly reduced in size and slightly flattened; pronotum (Fig. 4D) relatively shorter and broader (ratio PW/PL = 1.50), lateral margin abruptly bisinuate in basal one-fourth; subapical sinuation of elytral lateral margin(Fig. 5D) very shallow, elytral epipleuron smoothly and narrowly tapered to merger with elytral lateral margin, elytral interval 3 with one seta in apical onethird; females with hemisternites of sternum VIII entire (Fig. 7D), without medial membranous areas, spermathecal gland relatively short and distinctly swollen at anterior end (Fig. 8D).

Comparisons with other species. - Using the key of Liang and Yu (2002), the single known specimen of this species runs to couplet 4, but no further because it conforms to neither alternative in that couplet. Among adults of all species included in the key, A. splendida adults are apparently unique in having elytral intervals $1,3,5$, and 7 both distinctly convex and with nearly effaced microsculpture, at least at the centers of those intervals.

Adults of A. splendida apparently are easily distinguished from those of A. abrupta, A. yuae, and A. exochopleurae by the brilliant greenish metallic reflection on the head, pronotum, and ely-
tra (coppery metallic reflection with greenish highlights in the other species), slightly smaller and flatter eyes (Fig. 3; eyes larger and more convex in the other species, Figs. 1 and 2), pronotum shorter and broader basally (Fig. 4D; longer and more narrowed basally in the other species, Figs. 4A, B, and C), with lateral margin abruptly bisinuate in basal one-fourth (shallowly and gradually sinuate in A. yuae (Fig. 4B), straight or shallowly and gradually sinuate in $A$. exochopleurae (Fig. 4C), and moderately deeply and abruptly sinuate in A. abrupta (Fig. $4 \mathrm{~A})$ ), elytral intervals $1,3,5$, and 7 with microsculpture nearly effaced at least at interval centers (microsculpture distinctly and shallowly or deeply impressed in the other species), subapical sinuation of the elytral lateral margin very shallow (deep in the other species), and females with hemisternites of sternum VII entire (Fig. 7D), without medial membranous areas (with deeply incised membranous area medially in the other species, Figs. 7A, B, and C), and spermathecal gland relatively short (Fig. 8D; longer in the other species, Figs. 8A, B, and C).

From adults of all the remaining species, those of A. splendida can be distinguished by their slightly smaller and flatter eyes (larger and more convex in all other species), and the lateral pronotal margin bisinuate in the basal one-


Figure 3. Digital photograph of holotype of Aristochroa splendida sp. nov., dorsal aspect; scale line $=1.0 \mathrm{~mm}$. fourth (straight or slightly to deeply sinuate in all other species). They are also distinguished from adults of all other species except $A$. morvani by their short and shallow frontal furrows (longer and deeper in all other species), and from adults of A. kangdingensis, the species in which the pattern of elytra microsculpture appears to be most similar, by their black tibiae and catenate elytral intervals 4 and 6 (tibiae brown and intervals 4 and 6 entire, not catenate, in A. kangdingensis).

Description.- Total length holotype female 12.9 mm , ratio $\mathrm{EL} / \mathrm{PL}=2.73$. Head, pronotum, elytra, venter, and tibiae black; dorsal surface of head and pronotum with brilliant greenish metallic reflection without coppery highlights: elytral intervals $1,3,5$, and 7 brilliant coppery, intervals 2, 4, 6 and 8 and all other elytral areas brilliant greenish (Fig. 3).

HEAD. Eyes slightly flattened, slightly reduced in size, diameter less than twice length of angulate tempora. Frons densely and very finely punctulate: frontal furrows short and shallow, slightly divergent posteriorly and terminated posteriorly as a few vaguely-defined wrinkles, smooth, impunctate. Vertex smooth. Two pairs of supraorbital setae present. Glossal sclerite with two pairs of apical setae.

Thorad. Pronotum (Fig. 4D) short and broad. ratio PW/PL $=1.50$, greatest width slightly anterior to middle; lateral margin smoothly arcuate from apical angles to one-fourth from base, then slightly and more abruptly bisinuate to bluntly denticulate hind angles, with shallow crenulations


Figure 4. Pronotum, dorsal aspect; scale lines $=1.0 \mathrm{~mm}$. A. Aristochroa abrupta Kavanaugh and Liang. B. Aristochroa yuae sp. nov. C. Aristochroa exochopleurae sp. nov. D. Aristochroa splendida sp. nov.
present along entire margin, densest near basal angles; hind angles slightly obtuse; lateral margin with three setae at and anterior to middle; pronotal disc with just a few faintly etched transverse wrinkles, otherwise smooth with sparse, minute punctulae over entire surface, microsculpture comprised of very shallowly impressed, distinctly transverse meshes barely visible in some areas; basal foveae moderately deep, with two longitudinal sulci present; area between sulci distinctly convex, smooth, impunctate, broad anteriorly, slightly narrowed posteriorly by convergence of sulci; inner sulcus about 1.5 times as long as outer sulcus, distinctly deflected laterally near base, smooth and impunctate; outer sulcus slightly curved (anterior and posterior ends slightly deflected medially), smooth and impunctate; laterobasal ridge (external to outer sulcus) moderate in width. Prosternum with median longitudinal impression present but faint, transverse groove anterior to coxae present as vague, disrupted depression. Proepisternum, mesepisternum, and metepisternum impunctate. Elytra more or less symmetrically subovoid, ratio EL/EW $=1.39$, widest at middle; subapical sinuation very shallow; elytral epipleuron gradually and narrowly tapered to merger with lateral elytral margin (Fig. 5D); elytral microsculpture comprised of isodiametric meshes, very faintly impressed on intervals $1,3,5$, and 7 , moderately impressed on intervals $2,4,6$, and 8 ; basal margination slightly concave anteriorly, slightly wavy, basal and lateral marginations joined at distinct


Figtre 5. Left elytron, showing apical end of elytral epipleuron. internal plica, and subapical sinuation of lateral margin. posterolateral oblique aspect: scale lines $=1.0 \mathrm{~mm}$. A. Aristochroa abrupta Kavanaugh and Liang. B. Aristochroa yuae sp. nov. C. Aristochroa exochopleurae sp. nov. D. Aristochroa splendida sp. nov.
obtuse angle at humerus: humeral tuberosity distinctly present: striae moderately impressed, finely and distinctly punctate; elytral intervals $1,3,5,7$, and 8 moderately convex, intervals 2,4 , and 6 slightly convex: intervals 4 and 6 catenate. especially subapically: intervals $1.3,5$, and 7 distinctly broader than intervals $2,4,6$, and 8 , width of interval 3 at middle 1.7 times width of interval 4; interval 3 with one seta present in apical one-third: interval 5 merged with interval 7 at apical onefourth; intervals 4.5, and 6 not fused posteriorly.

Abdonen. Sternum VII with two pairs of apical paramedial setae (in female). Female genitalia with hemisternites of sternum V'III entire medially (without medial membranous areas) (Fig. 7D); gonostylus (stylomere II) of ovipositor broad. arcuate; spermatheca pointed and slightly coiled on anterior end: spermathecal gland short. only slightly longer than spermatheca, tubular, distinctly swollen at anterior end (Fig. 8D).

Sexcal dimorphisy.- Unknown (holotype female is the only specimen known at this time).
Geographical distribltiox.- Fig. 12A and C. At present, known only from crest of the Gaoligongshan, on the China/Myanmar border, at the top of the drainage system of the north fork


Figure 6. Median lobe of aedeagus of male; A-C, left lateral aspect, D-F, ventral aspect; scale lines $=1.0 \mathrm{~mm}$. A and D. Aristochroa abrupta Kavanaugh and Liang. B and E. Aristochroa yuae sp. nov. C and F. Aristochroa exochopleurae sp. nov.
of Yamu He (Yamu River) in Lumadeng Township, Fugong County, Yunnan Province, China (for locality information, see label data for type specimen).

Geographical relations with congeners. - The known geographical range of A. splendi$d a$ is distinctly allopatric with respect to all other known species of Aristochroa except A. yuae sp. nov. (Fig. 12 C ). The single record for $A$. splendida is from the ridge crest of the Gaoligongshan, at 3710 m , an area immediately above the drainage system (Yamu River system) in which A. yuae appears to be restricted, at elevations ranging from 2800 to 3300 meters, on the eastern slope of the range. Additional sampling is needed to determine if these two species occur together at intermediate elevations here or elsewhere. The nearest known localities for A. abrupta and A. exochopleurae


Figure 7. Sternum VIII, ventral aspect; scale lines $=1.0 \mathrm{~mm}$. A. Aristochroa abrupta Kavanaugh and Liang. B. Aristochroa yuae sp. nov. C. Aristochroa exochopleurae sp. nov. D. Aristochroa splendida sp. nov.
are about 46 kilometers north and 132 kilometers south, respectively, of the known range of $A$. splendida.

Geographical variation.- Unknown; known at present only from a single specimen from a single locality.

Habitat distribution. - The type specimen was collected from under a stone on the crest of the Gaoligongshan (Fig. 11), at 3710 meters elevation, along the edge of a trail through a mosaic of low (up to one meter high) thickets of shrubby Rhododendron spp. and/or bamboo and patches of moist alpine meadow vegetation.

Etymology:- This species epithet is a feminine nominative singular adjective, derived from the Latin splendidus, meaning bright or shining, in reference to the brilliant metallic reflection and luster of the dorsal surface of the single known adult of this species.

## Acknowledgements

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FIGURE 8. Female genitalia, ventral aspect; $c o=$ common oviduct, $s p=$ spermatheca, and $\mathrm{spg}=$ spermathecal gland; scale lines $=1.0 \mathrm{~mm}$. A. Aristochroa abrupta Kavanaugh and Liang. B. Aristochroa yuae sp. nov. C. Aristochroa exochopleurae sp. nov. D. Aristochroa splendida sp. nov.






Figure 10. Photographs of habitat for Aristochroa exochopleurae sp. nov., eastern slope of the Gaoligongshan, just east of Fengxue Yakou (pass) at 3150 m , in Lushui County, Yunnan China, mid-May, 2005. A. Northeast-facing slope, covered by mixed bamboo/Rhododendron thickets with scattered conifers at higher elevations (in distance). B. View of upper slope along roadcut, with thick cover of shrubby Rhododendron spp. and bamboo in thickets.


Figure 11. Photograph of habitat for Aristochroa yuae sp. nov.; view looking south along the crest of the Gaoligongshan, at China/Myanmar border, 3700 m . in Fugong County. Yunnan China, mid-August, 2004; trailside vegetation includes lowgrowing bamboo and Rhododendron spp. thickets and assorted ericaceous and herbaceous plants in patches of moist or dry meadow.


FIGURE 12. Map illustrating distributions of known localities for Aristochroa species in the Gaoligongshan, western Yunnan Province, China. A. Map of Gaoligong region illustrating geographical relationships of known distributions of all known species; grey area denotes extent of study area; blue circles $=A$. abrupta Kavanaugh and Liang; green circles $=A$. yuae sp. nov.; yellow circle $=$ A. splendida sp. nov.; and red circles $=$ A. exochopleurae sp. nov. B-D. Details of distributions of known records for each species plotted separately, color code same as in A.

## References

Kavanaugh D.H, and H.B. Liang. 2003. A new species of Aristochroa Tschitschérine (Coleoptera: Carabidae) from Yunnan, China. Proceedings of California Academy of Sciences, ser. 4, 54(14):239-245.
Liang, H.B., and P.Y. Yu. 2002. A new species of Aristochroa Tschitschérine (Coleoptera: Carabidae), with a key to species for the genus. Coleopterists Bulletin 56:144-151.
Sciaky, R., and D.W. Wrase. 1997. Twenty-nine new taxa of Pterostichinae from Shaanxi (Coleoptera, Carabidae). Linzer Biologische Beiträge 29(2):1087-1139.
Straneo, S.L. 1938. Nuova specie del genere Aristochroa Tschit. Bollettino della Società Entomologica Italiana 70:122-123.
Tian M.Y. 2004. Descriptions of new species of the genus Aristochroa Tschitschérine, 1898, from Yunnan, Sichuan and Qinghai provinces, China. Coléoptères 10(20):235-246.
Tschitschérine, T. 1898. Matériaux pour servir à l'édude des Féroniens, IV. Horae Societatis Entomologicae Rossicae 32:70-77.
Tschitschérine, T. 1903. Species nova generis Aristochroa Tsch. (Coleoptera, Carabidae). Revue Russe de Entomologie 3-4:224-225.
Xie, W.P., and P.Y. Yu. 1993. Classification of the genus Aristochroa in China (Coleoptera: Carabidae). Acta Scientiarum Naturalium Universitatis Pekinensis 29(2):174-183.
Zamotallov, A.S., and D.N. Fedorenko. 2000. New species of the genus Aristochroa Tschitschérine, 1898 (Coleoptera: Carabidae) from west China. Russian Entomological Journal 9:103-112.

## Short Communications

Replacement Name Proposed for the Genus Simpsonella Stiasny, 1940 (Octocorallia: Chrysogorgiidae), Preoccupied by Simpsonella Cockerell, 1903 (Bivalvia: Unionddae). - The International Code of Zoological Nomenclature (Fourth Edition, 1999:57) states, "53.2. Homonyms in the genus group. In the genus group, two or more available names established with the same spelling are homonyms. Example. The generic name Noctua Linnaeus, 1758 (Lepidoptera) and Noctua Gmelin, 1771 (Aves) are homonyms." On the other hand, species of animals can share generic names with plants. An example is the genus Mimulus (Crustacea: Decapoda and Anthophyta: Scrophulariaceae).

## Bivalvia: Unionidae

The type species of the valid freshwater mussel genus Simpsonella, is Anodonta purpurea Valenciennes, 1821.

## Synonomy:

Non Anodonta Lamarck, 1799, Valenciennes, 1821.
Dalliella C.T. Simpson, 1900 (preoccupied by Dalliella Cossmann, 1895; Gastropoda: Prosobranchia).
Simpsonella Cockerell, 1903.

## Octocorallia: Chrysogorgiidae

## Synonomy:

Non Juncella (misspelling of Junceella Valenciennes, 1855), Hickson, 1904:231.
Hicksonella J.J. Simpson, 1910: 682 (preoccupied by Hicksonella Nutting, 1910; Octocorallia: Gorgoniidae) Non Radicipes Stearns, 1883, Kükenthal, 1919:545.
Simpsonella Stiasny, 1940:31. Williams, 1992a:253; 1992b:376, 395; 1992c:379 (preoccupied by Simpsonella Cockerell, 1903; Bivalvia: Unionidae)
Helicogorgia Bayer, 1981:902, 938 (this name was originally proposed to replace Hicksonella J.J. Simpson, 1910, which was preoccupied; but the author was unaware of the published accounts of either Simpsonella Stasny, 1940 or Simpsonella Cockerell, 1903).

Replacement Name: Helicogorgia Bayer, 1981.
Figures 1, 2.
This alcyonacean genus, composed of five species, is distributed in the western Indian Ocean, along the East African coast from Dar es Salaam and Zanzibar (Tanzania) in the north, to East London (South Africa) in the South; bathymetric range 66-775 meters:

1. Helicogorgia spiralis (Hickson, 1904) [type species] - South Africa
2. Helicogorgia flagellata (J.J. Simpson, 1910) - South Africa
3. Helicogorgia capensis (J.J. Simpson, 1910) - South Africa
4. Helicogorgia squamifera (Kükenthal, 1919) - Zanzibar and South Africa
5. Helicogorgia ramifera (Williams, 1992) - South Africa

Nomenclatural History.- Valenciennes (1821) described a new species of Asian freshwater mussel as Anodonta purpurea. Simpson (1900) considered this taxon to belong to a previously undescribed genus, and named it Dalliella. Cockerell (1903) observed that the name Dalliella C.T. Simpson, 1900, was preoccupied by Dalliella Cossmann, 1895 (a gastropod prosobranch), and proposed the generic name Simpsonella as a replacement. Hickson (1904) described a new species of
gorgonian octocoral as Juncella spiralis (Juncella is a misspelling of Junceella Valenciennes, 1855). J.J. Simpson (1910) considered this taxon to belong to a different genus and provided the new name Hicksonella spiralis, apparently unaware of Hicksonella Nutting, 1910. He also described two additional species, Hicksonella flagellata and Hicksonella capensis. Prior to this (but in the same year), Nutting (1910) proposed the name Hicksonella for a gorgonian octocoral in the family Gorgoniidae. Kükenthal (1919) described a fourth species as Radicipes squamiferus from Tanzania, and placed it in the chrysogorgiid gorgonian genus Radicipes Stearns, 1883. Stiasny (1940), presumably unaware of Cockerell's replacement name, recognized the priority of Hicksonella Nutting, 1910, and proposed the replacement name Simpsonella. Bayer (1981), not aware of Stiasny's replacement name, proposed the name Helicogorgia for Hicksonella Simpson, 1910. Williams (1992c) revised the genus of four species and added a fifth species, Simpsonella ramifera. He also recognized Radicipes squamiferus as a synonym of Simpsonella squamifera and the priority of Stiasny's replacement name Simpsonella over Helicogorgia (but was also unaware of Simpsonella Cockerell, 1903)

In March of 2006, Joel Hallan brought to my attention the fact that the freshwater mussel genus Simpsonella of Cockerell (1903) has priority over the gorgonian name Simpsonella of Stiasny (1940). Since Bayer (1981) already provided the replacement name Helicogorgia, at the time unaware of either Simpsonella Cockerell. 1903, or Simpsonella Stiasny, 1940, Helicogorgia Bayer, 1981, is here proposed as the valid replacement name for Simpsonella Stiasny, 1940.


Figure 1. Helicogorgia spiralis (Hickson. 1904), type species of the genus. A. Whole colony: scale bar $=25 \mathrm{~mm}$. B. Cleared axis of another colony; scale bar $=50 \mathrm{~mm}$. C. Diagram of a partial colony showing polyps and a portion of bare axis; scale bar $=4 \mathrm{~mm}$. D. Scanning electron micrograph showing polyps on a portion of a colony: scale bar $=0.75$ mm . A and C from Williams. 1992a: B and D from Williams. 1992c.


Figure 2. Map of central and southern Africa showing the known distribution of the genus Helicogorgia. Black triangles represent collecting stations.

## Acknowledgments

I am grateful to Joel Hallan (Austin, Texas) for alerting me to the fact that Simpsonella Stiasny, 1940 (a gorgonian octocoral), is preoccupied by Simpsonella Cockerell, 1903 (a genus of freshwater mussel).

## Literature Cited

BAYER, F.M. 1981. Key to the genera of Octocorallia exclusive of Pennatulacea, (Coelenterata, Anthozoa), with diagnoses of new taxa. Proceedings of the Biological Society of Washington 94(3):902-947
Cockerell, T.D.A. 1903. Some Homonymous Generic Names. The Nautilus 16(10):118.
Hickson, S.J. 1904. The Acyonacea of the Cape of Good Hope. Part 2. Marine Investigations in South Africa 3:211-239.
International Trust for Zoological Nomenclature. 1999. International Code of Zoological Nomenclature, $4^{\text {th }}$ ed.. 1999. The International Trust for Zoological Nomenclature, c/o The Natural History Museum, Cromwell Road, London SW7 5BD, UK. 306 pp.
Lamarck, J.B. 1799. Prodrome d'une nouvelle classification des Coquilles. Mémoires de la Société d'histoire naturelle de Paris 1799:63-91.
Kükenthal, W. 1919. Gorgonaria. Wiessenschafiliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer 'Valdivia', 1898-1899 13(2):1-946.
Nuttivg, C. C. 1910. The Gorgonacea of the Siboga Expedition. IV. The Plexauridae. Siboga-Expeditie (Livr. 48), Monograph 13b1:1-20.

Simpson, C.T. 1900. Synopsis of the Naides, or pearly fresh-water mussels. Proceedings of the United States National Museum 22 (1205):501-1075.
Sampson, J.J. 1910. Hicksonella, a new gorgonellid genus. Journal of the Royal Microscopical Society 1910 (6):681-692.

Stiasny, G. 1940. Alcyonaria und Gorgonaria von Dud Afrika aus der Sammlung des South African Museum, Cape Town. Verhandelingen der K. nederlandsche akademie van wetenschappen, Afdeeling Natuurkunde, Tweede Sectie 39(3):1-37.
Valenciennes, A. 1821. In: Humboldt, A. von and A. Bonpland, Voyage aux régions équinoxiales du nouveau continent, fait en 1799, 1800, 1801, 1802, 1803 et 1804, vol. 2, part 11.
Valenciennes, A. 1855. Extrait d'une monographie de la famillé des Gorgonidées de la classe des polypes. Compte rendu de l'Académie des sciences, Paris 41:7-15.
Williams, G.C. 1992a. The Alcyonacea of southern Africa. Gorgonian Octocorals (Coelenterata, Anthozoa). Annals of the South African Museum 101(8):181-296.
Williams, G.C. 1992b. Biogeography of the octocorallian coelenterate fauna of southern Africa. Biological Journal of the Linnean Society 46(4):351-401.
Williams, G. C. 1992c. Revision of the gorgonian genus Simpsonella (Octocorallia: Chrysogorgiidae) from the western margin of the Indo-Pacific, with the description of a new species from southeastern Africa. Zoological Journal of the Linnean Society 105:377-405.
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## Notes and Comments on Some Eastern Atlantic Snake Eels (Angullliformes:

Ophichthidae). - Abstract: Pseudomyrophis nimius Böhlke (1960) is first reported from off west Africa. Microrhynchus epinepheli Blache and Bauchot (1972) is synonymized with Sphagebranchus foresti Cadenat and Roux (1964). Microrhynchus Blache and Bauchot (1972) is synonymized with Phaenomonas Myers and Wade (1941). Phaenomonas is expanded to include species which lack all fins. Ophichthus karreri Blache (1975) is synonymized with Ophichthys serpentinus Seale (1917).

During the preparation of the chapter on the Snake eels, Worm eels, and Sand eels (family Ophichthidae) for the upcoming publication of the FAO Living Marine Resources of the Eastern Central Atlantic (Kent Carpenter, editor), I have made taxonomic decisions on several eel species of questionable identity. As well, I have discovered new records of species previously unreported from that area. The FAO series does not allow an opportunity to explain those actions or specimens, so to that end they will be treated in this brief paper.

## Materials and Methods

Measurements, techniques, and anatomical definitions follow that of McCosker et al. (1989: 257). Vertebral counts (which include the hypural) were taken from radiographs. The mean vertebral formula (MVF) is expressed as the average of predorsal, preanal, and total vertebrae. Specimens are deposited at the California Academy of Sciences, San Francisco (CAS), the Los Angeles County Museum of Natural History (LACM), the Muséum National d’Histoire Naturelle, Paris (MNHN), and the Universitat Humboldt Museum fur Naturkunde, Berlin (ZMB). Institutional abbreviations follow the Standard Symbolic Codes for Institutional Research Collections in Herpetology and Ichthyology (Leviton et al. 1985).

## Taxonomy

A specimen of the benthic worm eel Pseudomyrophis nimius Böhlke (1960) was collected by Tomio Iwamoto during recent deepwater assessment cruises off Angola aboard the $R / V \mathrm{Dr}$. Fridtjof Nansen. Described from the Gulf of Mexico and subsequently known from the northern Gulf of Mexico and from the Florida Atlantic at depths of $320-755 \mathrm{~m}$, this appears to represent the first known Eastern Atlantic specimen (McCosker et al. 1989). It was captured at $06^{\circ} 55^{\prime} 00^{\prime \prime} \mathrm{S}$, $11^{\circ} 43^{\prime} 00^{\prime \prime}$ E. using an otter trawl with 1300 m wire out (trawling speed 3 knots) at $518-519 \mathrm{~m}$ depth during 2023-2055 on 21 April 2005. The specimen (CAS 224136) is a 367 mm TL male and has the following characteristics (measurements in mm ): head length. 25 ; trunk length 107 ; tail length 235: dorsal-fin origin 83: body depth behind gill openings 5.3: eye diameter: interorbital width 2.8; snout length 4.5 : upper jaw length 7.1 : and vertebral formula $+2 / 66 / 206$. It is uniform gray, although its chin and throat are slightly paler: its median fins are pale, becoming darker about 2 head lengths before the tail tip: and its head pores. lateral-line pores. and anterior nostrils are pale. Its pore pattern and dentition do not differ significantly from that of its western Atlantic conspecifics ( $c f$. McCosker et al. 1989. figs. 280-282). Its vertebral formula is less than the range of that of western Atlantic specimens (MVF 49-73-214. predorsal vertebrae 47-53. preanal vertebrae 71-75, total vertebrae 211-217). However. until additional eastern Atlantic specimens are examined, I am hesitant to assign it specific status.

The type specimens of Sphagebranchus foresti Cadenat and Roux (1964) and Microrhynchus epinepheli Blache and Bauchot (1972) have vexed systematic anguillologists since their capture and description. In describing M. epinepheli. a partially digested specimen taken from a grouper stomach. Blache and Bauchot created the new genus and included S. foresti as its type species. Species of Microrhynchus were said to lack fins totally. McCosker and Böhlke (1984) and McCosker et al.
(1989) subsequently referred those species to Ethadophis, but upon my reexamination of the type specimens of foresti (MNHN 1962-71, from the Cape Verde Islands) and epinepheli (MNHN 1964536, from Senegal) and the discovery of an additional and larger specimen of foresti from Ghana, I now consider them to belong in Phaenomonas Myers and Wade (1941) and therefore include Microrhynchus in the synonymy of that genus. The additional specimen of $P$. foresti (LACM 427011) was collected in 1974 off the continental shelf of Ghana over a 39 m mud bottom. The specimen has the following characteristics (measurements in mm): total length 437; head length 21.5; trunk length 285 ; tail length 130 ; body depth behind gill openings 5.6 ; eye diameter 0.7 ; interorbital width 2.7 ; snout length 4.1 ; upper jaw length 5.8 ; and vertebral formula $-/ 135 / 195$. Its pore pattern and dentition do not differ significantly from that of the holotypes of foresti and epinepheli. Careful examination of these three specimens indicates that they are conspecific and that the type specimen of foresti has a very low and short dorsal fin, beginning approximately 9.5 mm behind the snout tip and extending approximately 43 mm from the snout tip. Neither fins nor pterygiophores are visible by radiography on the other two specimens. They have the following total vertebral numbers: type of foresti 187; type of epinepheli 192; and Ghana specimen 194.

An additional Atlantic species of Phaenomonas, P. longissima (Cadenat and Marchal 1963), is known from St. Helena and Ascension islands and from Brazil. It differs from P. foresti in its vertebral number (206-216 vs. 187-194) and in that the six known specimens (McCosker et al. 1989) have a small but apparent dorsal fin, originating mid-head and extending about three head lengths behind it. I am hesitant at this time to synonymize foresti with longissima until additional specimens of eastern Atlantic Phaenomonas are obtained.

In that these eastern Atlantic specimens of Phaenomonas vary in the presence or absence of a minuscule dorsal fin, but share the generic characteristics of the three other species of Phaenomonas (McCosker 1975; McCosker et al. 1989), it is appropriate to modify the generic diagnosis of Phaenomonas as follows: dorsal fin absent in some specimens, small and low if present, beginning in the anterior head region and extending to the anterior trunk region.

Ophichthus karreri Blache (1975), known from a single specimen captured in 390 m off Namibia ( $26^{\circ} 32^{\prime} \mathrm{S}, 14^{\circ} 13^{\prime} \mathrm{E}$ ), has not been reported upon since its description. After examining numerous specimens of Ophichthus serpentinus Seale (1917), described from the Cape of Good Hope, I am convinced that $O$. karreri is a junior synonym. Although I have been unable to examine the holotype of $O$. karreri (ZMB 22065), its description agrees in coloration, dentition, morphometrics and vertebral number ( 165 , vs. 162-167 for $O$. serpentinus) with that of $O$. serpentinus. Ophichthus serpentinus is not uncommon at depths of 235-490 m off Namibia and South Africa, and also includes Ophichthus bennettai McCosker (1986) in its synonymy.

## Acknowledgments

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## LITERATURE CITED

BLache, J. 1975. Contribution à la connaissance des Poissons Anguilliformes de la côte occidentale d'Afrique. $15^{\text {e }}$ note: compléments aux familles des Muraenidae, des Heterenchelyidae et des Ophichthidae. Bulletin de l'IFAN, sér. A, 37(3):708-740.
Blache, J., And M.L. Bauchot. 1972. Contribution à la connaissance des Poissons Anguilliformes de la côte
occidentale d'Afrique. 13e note: les genres Verma, Apterichtus, Ichthyapus, Hemerorhinus, Caecula, Dalophis avec la description de deux genres nouveaux (Fam. des Ophichthidae). Bulletin de l'IFAN, sér. A, 34(3):692-773.
Böнlкe, J.E. 1960. A new ophichthid eel of the genus Pseudomyrophis from the Gulf of Mexico. Notulae Naturae No. 329: 8 pp.
Cadenat, J., and E. Marchal. 1963. Résultats des campagnes océanographiques de la Reine-Pokou aux iles Sainte-Hélène et Ascension. Poissons. Bulletin de l'IFAN, sér. A, 25(4):1235-1315.
Cadenat, J., and C. Roux. 1964. Résultats scientifiques des campagnes de la "Calypso". Mes du Cap Vert. Poissons téléostéens. Annals Institute Océanographique Monaco, (N.S.):81-102.
Leviton, A.E., R.H. Gibbs, Jr., E. Heal, and C.E. Dawson. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resources collections in herpetology and ichthyology. Copeia 1985:802-832.
McCosker, J.E. 1975. The eel genus Phaenomonas (Pisces, Ophichthidae). Pacific Science 29:361-363.
McCosker, J.E. 1986. A new snake eel, Ophichthus bennettai, (Pisces: Ophichthidae) from off western South Africa. Special Publications of the JLB Smith Institute of Ichthyology, no. 39.4 pp.
McCosker, J.E., E.B. Böhlke, and J.E. Böhlke. 1989. Family Ophichthidae. Pages 254-412 in Fishes of the Western North Atlantic, Part Nine, Vol. One: Orders Anguilliformes and Saccopharyngiformes. Sears Foundation for Marine Research, Yale University, New Haven, Connecticut, USA.
McCosker, J.E., And J.E. Böhlke. 1984. A review of the snake eel genera Gordiichthys and Ethadophis, with descriptions of new species and comments on related Atlantic bascanichthyins (Pisces: Ophichthidae). Proceedings of the Academy of Natural Sciences of Philadelphia 136:32-44.
Myers, G.S., and C.B. Wade. 1941. Four new genera and ten new species of eels from the Pacific coast of tropical America. Allan Hancock Pacific Expedition 9(4):65-111.
Seale, A. 1917. New species of apodal fishes. Bulletin of the Harvard Museum of Comparative Zoology 61(4): 79-94

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    ${ }^{6}$ Address for correspondence.

[^1]:    ${ }^{7}$ Additional counts and measurements for P. persicus and P. fieldi are given by Gasperetti (1988:354, table 15).
    ${ }^{8}$ Head damaged

[^2]:    Figure 20. Palpibracus pilosus (Macquart, 1851); dorsum of mesothorax Figure 21. Palpibracus pilosus (Macquart, 1851); pleurae
    Figure 22. Palpibracus pilosus (Macquart, 1851); dorsum of abdomen
    Figure 23. Palpibracus schlingeri Couri and Penny, new species; dorsum of mesothorax
    Figure 24. Palpibracus schlingeri Couri and Penny, new species; pleurae
    Figure 25. Palpibracus schlingeri Couri and Penny, new species; dorsum of abdomen
    Figure 26. Palpibracus spicatus (Malloch, 1934); dorsum of mesothorax
    Figure 27. Palpibracus spicatus (Malloch, 1934); pleurae
    Figure 28. Palpibracus spicatus (Malloch, 1934); dorsum of abdomen
    Figure 29. Palpibracus trivittatus (Malloch, 1934); dorsum of mesothorax
    Figure 30. Palpibracus trivittatus (Malloch, 1934); pleurae
    Figure 31. Palpibracus trivittatus (Malloch, 1934); dorsum of abdomen
    Figure 32. Palpibracus vittatus Couri and Penny, new species; dorsum of mesothorax
    Figure 33. Palpibracus vittatus Couri and Penny, new species; pleurae
    Figure 34. Palpibracus vittatus Couri and Penny, new species; dorsum of abdomen

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[^5]:    CT: Bristol. Fall Mountain CT: Bristol, Fall Mountain
    PA: Ridley Creek PA: Ridley Creek
    FL: Silver Springs PA: Ridley Creek SC: Aiken Co., Savannah River OR: Diamond Lake
    MD: Potomac River FL: Silver Springs
    IN. Randolph Co., Cabin Creek bog PA: Ridley Creek

    OR: Columbia River
    OR: Charleston
    Navicula bogotensis var. undulata M. Peragallo in Tempère \& Peragallo 1908 Navicula canoris Hohn \& Hellerman 1963 Navicula capsa Hohn 1961

    Navicula caractacus Hohn \& Hellerman 1963 Navicula caroliniana Patrick Navicula cascadensis Sovereign Navicula caterva Hohn \& Hellerman 1963

    Navicula cerneutia Hohn 1961
    Navicula cincta var. rostrata Reimer 1961 Navicula cinna Hohn \& Hellerman 1963

    Navicula columbiana Hustedt 1966
    Navicula complanatula Hustedt 1962

[^6]:    H:ANSP:53750 H:ANSP:44474 H:CAS:206009 H:ANSP:44466 H:ANSP:44460 H:ANSP:3628a H:ANSP:44264a H:CAS:205084 H:I.L.L.L.L-2-90 H:CAS:206010 H:CAS:205085 H:CAS:205081 H:ANSP:44469 H:CAS:205082 H:CAS:216061 H:ANSP:53749 H:CAS:205083 H:ANSP:53751 H:CAS:206011 H:ANSP:44467 $\stackrel{n}{c}$ 8
    0
    N
    亡
    ड
    i
     H:ANSP:44469

[^7]:    ${ }^{4}$ Research Associate, Department of Herpetology, California Academy of Sciences.

[^8]:    1915 Pachydactylus Weberi [part] Werner in Michaelsen, Land und Süsswasserfauna Deutsch-Sïdwest Afrikas I:334.
    1938 Pachydactylus weberi weberi ? FitzSimons, Ann. Transvaal Mus. 19:181.

[^9]:    la. Rostral and first supralabial enter nostril
    2 (serval complex)
    1b. Rostral excluded from nostril . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6 (weberi complex)
    2a. Juveniles with spotted juvenile pattern, adults with small, rounded, evenly-spaced spots with trace of two transverse lines or rows of spots on nape, snout strongly inflated laterally
    P. griffini

    2b. Juveniles with banded dorsal pattern, adult pattern not as above, snout not strongly inflated . 3
    3a. Juveniles dark-bodied with ashy nape and sacral bands. . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4
    3b. Juveniles with three or more cross bands . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5
    4a. Dorsal scalation largely atuberculate except for sacrum and lumbar region, tubercles not or feebly keeled, no tubercles on parietal table.
    P. serval

