

A NEW GENUS AND REDESCRIPTIONS FOR AFRICAN SPECIES
PREVIOUSLY PLACED IN *ACENTRELLA* (EPHEMEROPTERA: BAETIDAE)

C. R. LUGO-ORTIZ AND W. P. MCCAFFERTY

Department of Entomology, Purdue University, West Lafayette, IN 47907, U.S.A.

Abstract.—Within the Ephemeroptera family Baetidae, *Demoreptus*, new genus, is erected to accommodate *D. capensis* (Barnard), **new combination**, *D. monticola* (Crass), **new combination**, and *D. natalensis* (Crass), **new combination**. These species were originally described from southern Africa and assigned to *Acentrella* Bengtsson. *Demoreptus* is distinguished from *Acentrella* in the larval stage by having apicolaterally prolonged and attenuated fused incisors and relatively long, well-demarcated labial palp segments and in the adult stage by having a small, rounded process anteriorly on the mesoscutum. The larval stage of each species in *Demoreptus* is redescribed and a key to the species is provided. Analysis of interspecific relationships indicates that *D. capensis* is the most plesiotypic species, and that *D. natalensis* and *D. monticola* represent derived sister species.

Key Words: Ephemeroptera, Baetidae, *Demoreptus*, new genus, new combinations, Africa

The *Baetis* complex (Ephemeroptera: Baetidae) is a monophyletic grouping of genera comprised of *Acentrella* Bengtsson, *Baetiella* Uéno, *Baetis* Leach, *Barbaetis* Waltz and McCafferty, *Cymulabaetis* McCafferty and Waltz, *Gratia* Thomas, *Heterocloeon* McDunnough, *Labiobaetis* Novikova and Kluge, *Liebebiella* Waltz and McCafferty, *Platybaetis* Müller-Liebenau, and *Tanzaniella* Gillies. The complex is defined by the possession of the villopore, located on the ventral margin near the base of the larval femora (see, e.g. Waltz and McCafferty 1987: Figs. 1, 4, 5, 12, 17). Precise phylogenetic relationships within the complex, however, remain unknown.

The *Baetis* complex is relatively common and diverse in the Holarctic and Orient, but it is poorly known in the Neotropics and Australia. In the Afrotropics, the genera *Acentrella*, *Baetis*, *Pseudocloeon*, and *Tanzaniella* have been variously treated by Bar-

nard (1932, 1940), Crass (1947), Kimmins (1955, 1960), Demoulin (1970), Kopelke (1980), and Gillies (1991, 1993, 1994). Only one species has been described in the poorly known genus *Tanzaniella* (Gillies 1991), and, as Waltz and McCafferty (1987) and McCafferty and de Moor (1995) pointed out, the taxonomic status of species assigned to *Acentrella*, *Baetis*, and *Pseudocloeon* are in need of re-evaluation. This situation remains the same even though Gillies (1994) transferred all African species of *Pseudocloeon* to *Baetis*.

In this study, we address the African species that were described in the genus *Acentrella*: *A. capensis* Barnard, *A. monticola* Crass, and *A. natalensis* Crass. Those species proved to be referable to a new genus described herein. We additionally redescribe the larval stage of each species and provide a key for their identification. Materials examined are housed in the Albany Muse-

um (AM), Grahamstown, Eastern Cape Province, South Africa, and the Purdue Entomological Research Collection (PERC), West Lafayette, Indiana, U.S.A.

***Demoreptus* Lugo-Ortiz and McCafferty, new genus**

Larva (Fig. 1).—Head: Antennae 1.0–2.0× length of head capsule. Labrum with deep (Figs. 3, 16) or shallow (Fig. 9) anteromedial notch. Mandibles with apicolaterally prolonged and attenuated fused incisors, with distinct but poorly developed denticulation (Figs. 4, 5, 18, 19) or adenticulate and bladelike (Figs. 11, 12). Maxillae (Figs. 6, 13, 20) with palps two segmented. Labium (Figs. 7, 14, 21) with relatively long glossae and paraglossae; palps relatively long, extending beyond apices of glossae and paraglossae; palp segment 2 with poorly defined distomedial lobe; palp segment 3 width not exceeding that of apical width of segment 2 (Figs. 7, 21) or medially broader than apical width of segment 2 (Fig. 14). Thorax: Hindwingpads rudimentary to well developed. Legs with villopore present; femora with long, fine, simple setae dorsally; tarsi twisted; tarsal claws with single row of denticles and two subapical short, fine, simple setae. Abdomen: Terga without scales or scale bases; posterior marginal spines poorly defined. Gills on abdominal segments 1–7, platelike, poorly tracheated, marginally smooth (Fig. 23). Paraprocts (Figs. 8, 15, 24) without marginal spines. Two caudal filaments present, with abundant setae medially; medial caudal filament reduced to one segment.

Adult.—Mesoscutum with small, rounded anterior process in lateral view (Fig. 2). Forewings with paired marginal intercalaries. Hindwings present, except in males of *D. natalensis*; when present, with (Barnard 1932: Fig. 12b) or without (Crass 1947: Fig. 16b, 18b) costal process. Male genital forceps (Crass 1947: Fig. 17h) three segmented; segment 2 strongly bowed inwardly; segment 3 ellipsoidal.

Etymology.—We are honored in naming

this genus after Ferdinand C. de Moor, for his support of the study of aquatic insects in South Africa. The name consists of an arbitrary combination of letters that incorporates a Latinization of our colleague's last name and the Latin suffix *reptus* (to crawl), which is an allusion to the behavior of the larvae.

Type species.—*Demoreptus natalensis* (Crass), 1947: 72.

Species included.—*Demoreptus capensis* (Barnard), **new combination**; *D. monticola* (Crass), **new combination**; *D. natalensis* (Crass), **new combination**.

Distribution.—Lesotho; South Africa: Eastern Cape, KwaZulu-Natal, Mpumalanga, Western Cape.

Discussion.—Outgroup comparisons with *Baetis* indicate that *Demoreptus* probably arose from a *Baetis*-like ancestor whose adults had hindwings with a costal process and whose larvae possessed a labium with relatively long glossae, paraglossae, and palp segments; relatively short, ventrally oriented legs with straight tarsi; well-developed hindwingpads; terga with scales and well-developed posterior marginal spines; marginally serrate gills; and a well-developed medial caudal filament. *Demoreptus* shows the following apomorphies: apicolaterally prolonged and attenuated fused incisors; relatively long, outstretched legs with twisted tarsi; loss of tergal scales; reduction of tergal posterior marginal spines; loss of marginal serrations in the gills; and reduction of the medial caudal filament.

Demoreptus is phenotypically somewhat similar to the Holarctic and Oriental genus *Acentrella* as redefined by Waltz and McCafferty (1987). Larvae of both genera lack tergal scales and marginal spines on the gills and have outstretched legs with twisted tarsi, reduced marginal spines on the abdominal terga, and a reduced medial caudal filament. However, larvae of *Demoreptus* have relatively long labial palps (especially with regard to segment 2) with segments that are well demarcated (Figs. 7,

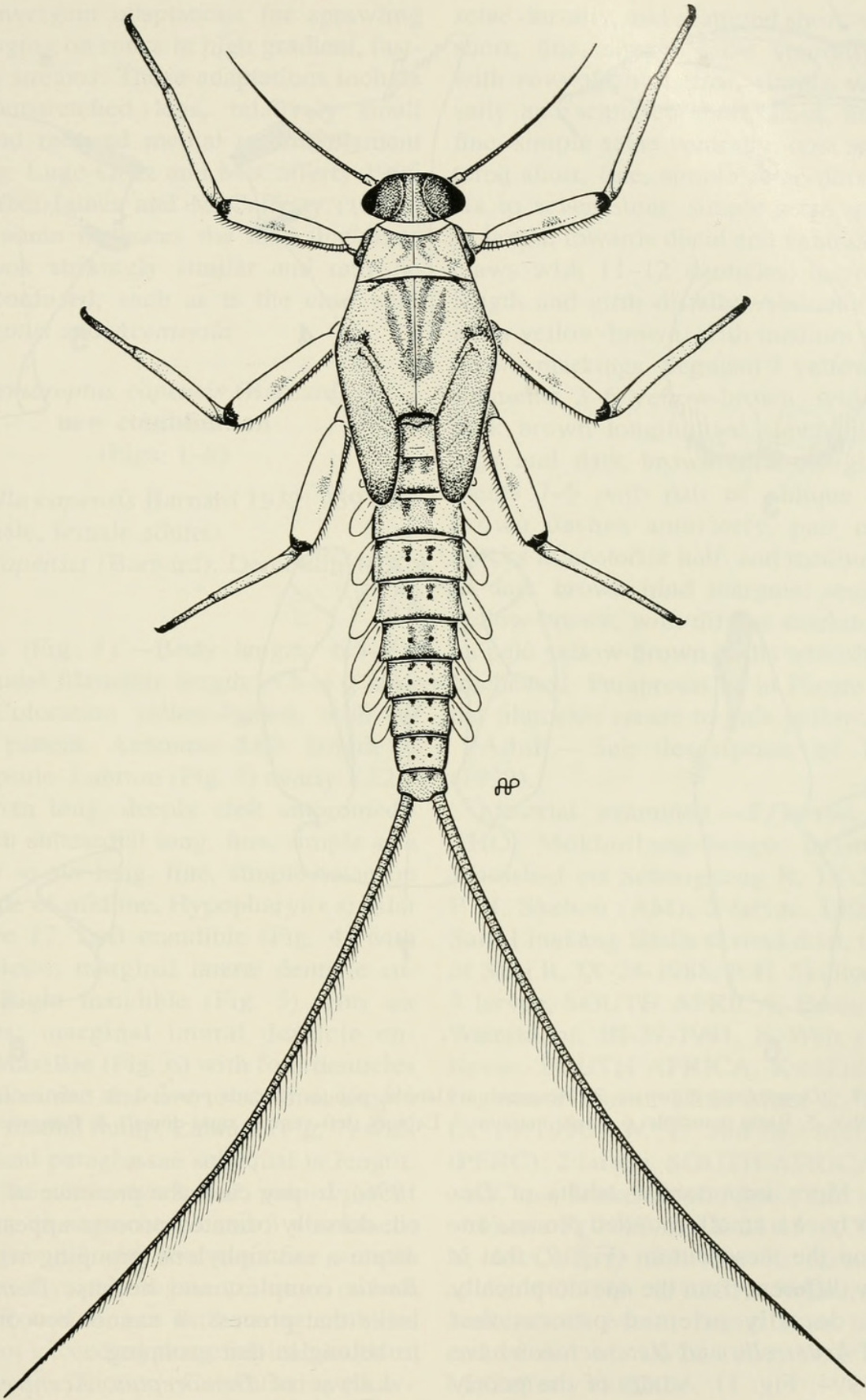
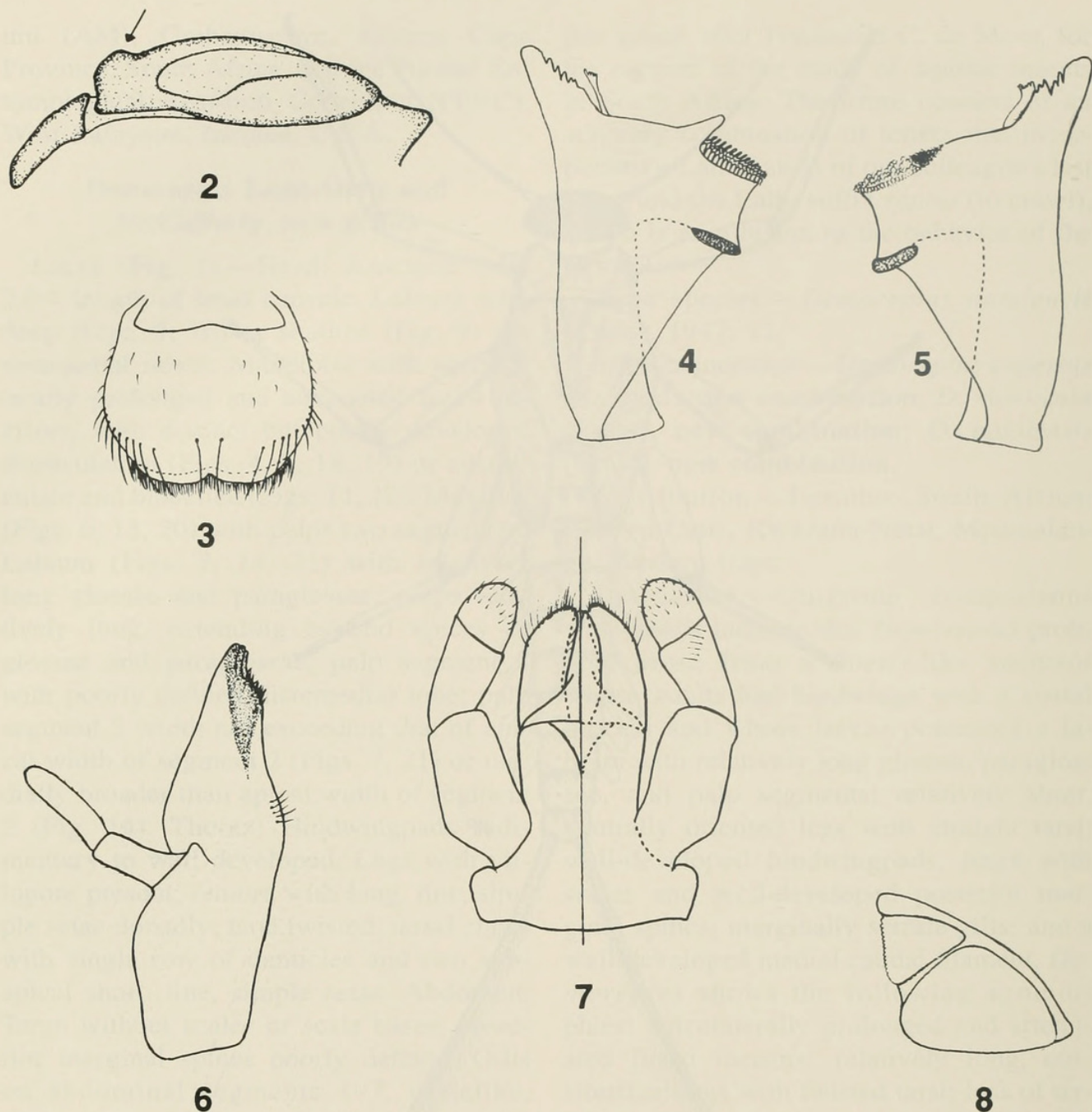


Fig. 1. *Demoreptus capensis*, larva (dorsal).



Figs. 2–8. *Demoreptus capensis*. 2, Mesoscutum (lateral; pointer towards process). 3, Labrum (dorsal). 4, Left mandible. 5, Right mandible. 6, Right maxilla. 7, Labium (left-ventral; right-dorsal). 8, Paraproct.

14, 21). More importantly, adults of *Demoreptus* have a small, rounded process anteriorly on the mesoscutum (Fig. 2) that is distinctly different from the apomorphically pointed, dorsally oriented process that adults of *Acentrella* and *Heterocloeon* have (Waltz 1994: Fig. 1). Adults of the poorly known Afrotropical genus *Tanzaniella* probably have that process (R. D. Waltz, pers. comm.), and it is possible that adults of the Oriental genus *Liebebiella* will also prove to have it once they are known (Waltz

1996). In any case, the presence of a pointed, dorsally oriented process appears to indicate a monophyletic grouping within the *Baetis* complex, and because *Demoreptus* lacks that process, it cannot be considered to belong in that grouping.

Larvae of *Demoreptus*, *Acentrella*, and certain other species of the *Baetis* complex, as well as distantly related genera such as the Afrotropical genus *Acanthiops* Waltz and McCafferty and the Panamerican genus *Baetodes* Needham and Murphy, show sev-

eral convergent adaptations for sprawling and clinging on rocks in high gradient, fast-running streams. Those adaptations include long, outstretched legs, relatively small gills, and reduced medial caudal filament (see, e.g. Lugo-Ortiz and McCafferty 1996 and Barber-James and McCafferty (1997), and in some instances the taxa that have them look strikingly similar and may be easily confused, such as is the case with *Demoreptus* and *Acentrella*.

Demoreptus capensis (Barnard),
new combination
 (Figs. 1–8)

Acentrella capensis Barnard 1932: 259 (larva; male, female adults).

Baetis capensis (Barnard): Demoulin 1970: 66.

Larva (Fig. 1).—Body length: 6.5–7.0 mm; caudal filaments length: 3.8–4.0 mm. Head: Coloration yellow-brown, with no distinct pattern. Antennae $2.0\times$ length of head capsule. Labrum (Fig. 3) nearly $1.22\times$ wider than long, deeply cleft anteromedially, with submedial long, fine, simple seta and five to six long, fine, simple setae on either side of midline. Hypopharynx similar to Figure 17. Left mandible (Fig. 4) with six denticles; marginal lateral denticle enlarged. Right mandible (Fig. 5) with six denticles; marginal lateral denticle enlarged. Maxillae (Fig. 6) with four denticles on galealaciniae and five to six fine, simple setae on medial hump. Labium (Fig. 7) with glossae and paraglossae subequal in length; paraglossae somewhat broad; palp segment 1 as long as segments 2 and 3 combined; palps segment 2 with five to six fine, simple setae dorsally; palp segment 3 more or less apically rounded, not bulbous or clublike (width not exceeding that of apical width of segment 2). Thorax: Coloration yellow-brown, with irregular medium brown markings. Hindwingpads long, almost reaching hind margin of abdominal segment 1. Legs yellow-brown; femora with poorly developed villopore, row of long, robust, simple

setae dorsally, and scattered short, stout and short, fine, simple setae ventrally; tibiae with row of short, fine, simple setae dorsally and scattered short, stout, and short, fine, simple setae ventrally; tarsi with scattered short, fine, simple setae dorsally and six to seven stout, simple setae increasing in length towards distal end ventrally; tarsal claws with 11–12 denticles, increasing in length and girth distally. Abdomen: Coloration yellow-brown, with medium and dark brown markings. Segment 1 yellow-brown; segments 2–6 yellow-brown, with pair of dark brown longitudinal submedial markings and dark brown hind margins; segments 7–9 with pair of oblique medium brown dashes anteriorly, pair of small specks in posterior half, and medium brown to dark brown hind margins; segment 10 yellow-brown, with diffuse markings. Sterna pale yellow-brown. Gills whitish, poorly tracheated. Paraprocts as in Figure 8. Caudal filaments cream to pale yellow.

Adult.—See description of Barnard (1932).

Material examined.—5 larvae, LESOTHO, Mokhotlong-Sengu, basin below Woolshed on Schonghong R, IX-25-1988, P. H. Skelton (AM); 2 larvae, LESOTHO, Sani-Linakeng Basin at road drift, tributary of Sani R, IX-24-1988, P. H. Skelton (AM); 3 larvae, SOUTH AFRICA, Eastern Cape, Waterkloof, III-27-1991, F. Weir (AM); 2 larvae, SOUTH AFRICA, KwaZulu-Natal, Highmoor Forest, Little Mooi R, 1800 m, IX-19-1990, W. P. and N. McCafferty (PERC); 2 larvae, SOUTH AFRICA, Western Cape, Jonkershoek Mnts., 2nd tributary of Eerste R, 1000 m, IX-28-1990, W. P. and N. McCafferty (PERC); 33 larvae, 1 ♀ adult, SOUTH AFRICA, Western Cape, Jonkershoek Mnts., Eerste R nr bridge at end of dirt rd, IX-28-1990, W. P. and N. McCafferty (PERC).

Discussion.—Larvae of *D. capensis* are distinguished from those of *D. natalensis* by the setation of the labrum (Fig. 3), the deeper and sharper denticulation of both mandibles (Figs. 4, 5), relatively short seg-

ment 2 and apically rounded segment 3 of the labial palps (Fig. 7), and long hindwingpads that almost reach the hind margin of abdominal segment 1. Adults of *D. capensis* are distinguished from those of *D. natalensis* by the presence of an acute costal process in the hindwings (Barnard 1932, 1940, Crass 1947).

Demoreptus monticola (Crass),
new combination
 (Figs. 9–15)

Acentrella monticola Crass 1947: 75 (larva; male, female adults).

Baetis monticola (Crass): Demoulin 1970: 68.

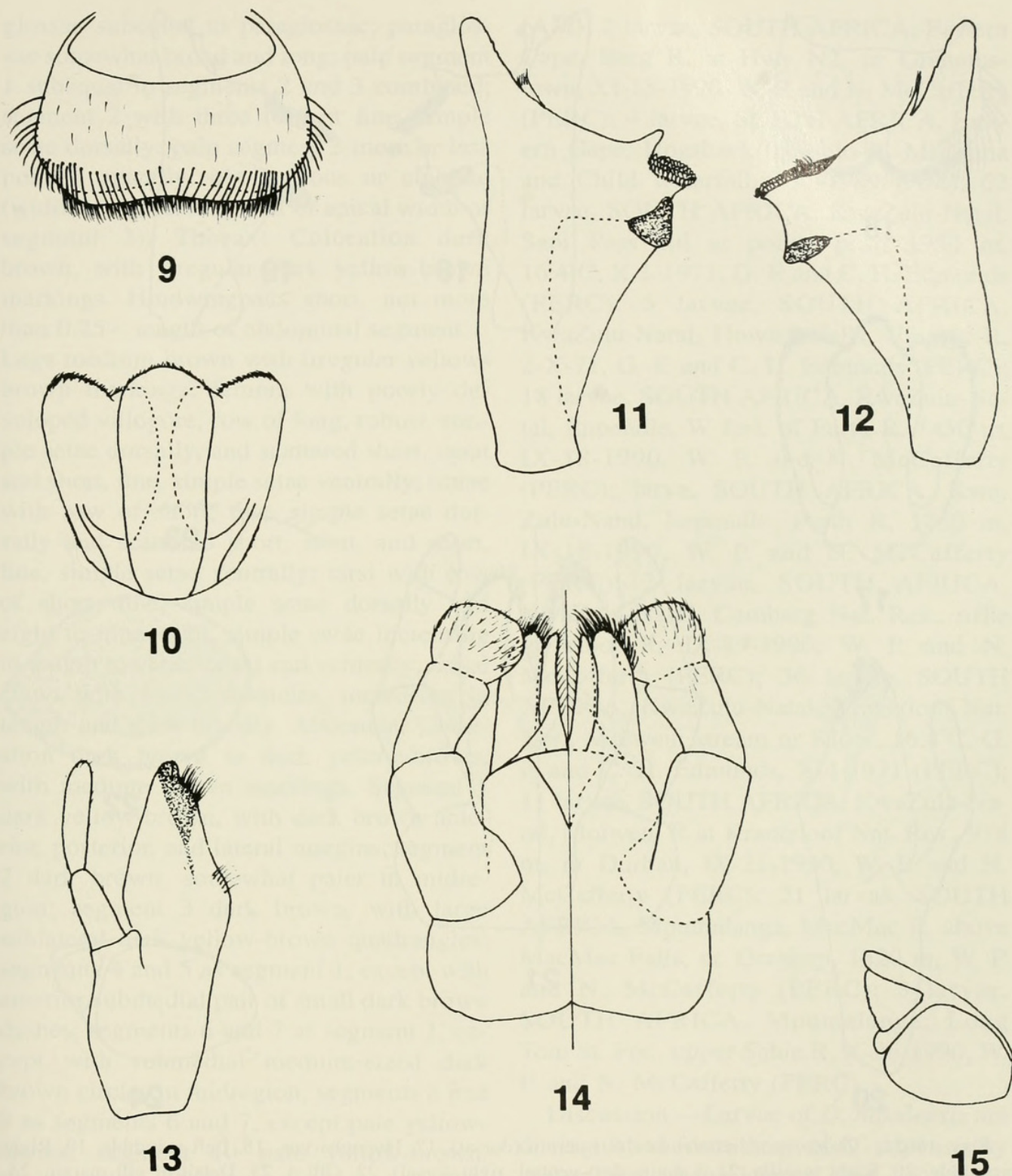
Larva.—Body length: 6.5–6.8 mm; caudal filaments length: 5.8–6.0 mm. Head: Coloration yellow-brown, with vermiform medium brown markings on frons. Antenna $1.5\times$ length of head capsule. Labrum (Fig. 9), $2.62\times$ wider than long, with shallow anteromedial emargination and 18–20 long, fine, simple setae on either side of midline; submedial seta absent. Hypopharynx as in Figure 10. Left mandible (Fig. 11) with incisors fused into one bladelike structure lacking denticles; prostheca apically denticulate. Right mandible (Fig. 12) with incisors fused into bladelike structure lacking denticles; prostheca apically pointed, with long, fine, simple setae medially. Maxillae (Fig. 13) with four denticles on galealaciniae and six to seven fine, simple setae on medial hump. Labium (Fig. 14) with glossae and paraglossae somewhat slender and subequal in length; palp segment 1 subequal to segments 2 and 3 combined; palp segment 2 with three to four fine, simple setae dorsally; palp segment 3 bulbous, clublike (medially broader than apical width of segment 2). Thorax: Coloration yellow-brown, with irregular medium brown markings. Legs yellow-brown; femora with poorly developed villopore, row of long, robust, simple setae dorsally, and scattered short, stout and short, fine, simple setae ventrally; tibiae with scattered short,

fine, simple setae dorsally and scattered short, stout, and short, fine, simple setae ventrally; tarsi with scattered short, fine, simple setae dorsally and six to seven stout, simple setae increasing in length towards distal end ventrally; tarsal claws with 11–12 denticles, increasing in length and girth distally. Abdomen: Coloration yellow-brown and dark brown. Segment 1 and 2 dark brown with large yellow-brown sub-lateral circular to oblong markings; segments 3–6 as segments 1 and 2, except with slender dorsal longitudinal medial yellow-brown streak; segments 7–9 yellow-brown, with submedial pair of dark brown specks in midregion and dark brown hind margins; segment 10 yellow-brown. Sterna cream to pale yellow-brown. Gills whitish, with single conspicuous tracheal trunk medially. Paraprocts as in Figure 15. Caudal filaments cream to pale yellow.

Adult.—See description of Crass (1947).

Material examined.—8 larvae, SOUTH AFRICA, Eastern Cape, Hogsback, Madonna and Child waterfall, X-7-1989 (AM); 142 larvae, SOUTH AFRICA, KwaZulu-Natal, Sani Pass Rd at police post, 1950 m, 16.4°C , X-1-1971, G. F. and C. H. Edmunds (PERC); 8 larvae, SOUTH AFRICA, KwaZulu-Natal, Umzimkulu R, between Underberg and Boesmansnek, 15.5°C , X-2-1971, G. F. and C. H. Edmunds (PERC); 5 larvae and ♀ subimago, SOUTH AFRICA, KwaZulu-Natal, Pietermaritzburg Nat. Bot. Garden, Dorspruit, IX-18-1990, W. P. and N. McCafferty (PERC); 31 larvae, SOUTH AFRICA, KwaZulu-Natal, Highmoor For., Little Mooi R, 1800 m, IX-19-1990, W. P. and N. McCafferty (PERC); 8 larvae, SOUTH AFRICA, Mpumalanga, 5 mi NE of Machadodorp, IX-22-1971, G. F. and C. H. Edmunds and H. J. Schoonbee (PERC).

Discussion.—Larvae of *C. monticola* are distinguished by the setation and shallow anterior emargination of the labrum (Fig. 9), adenticulate and bladelike mandibular incisors (Figs. 11, 12), and bul-



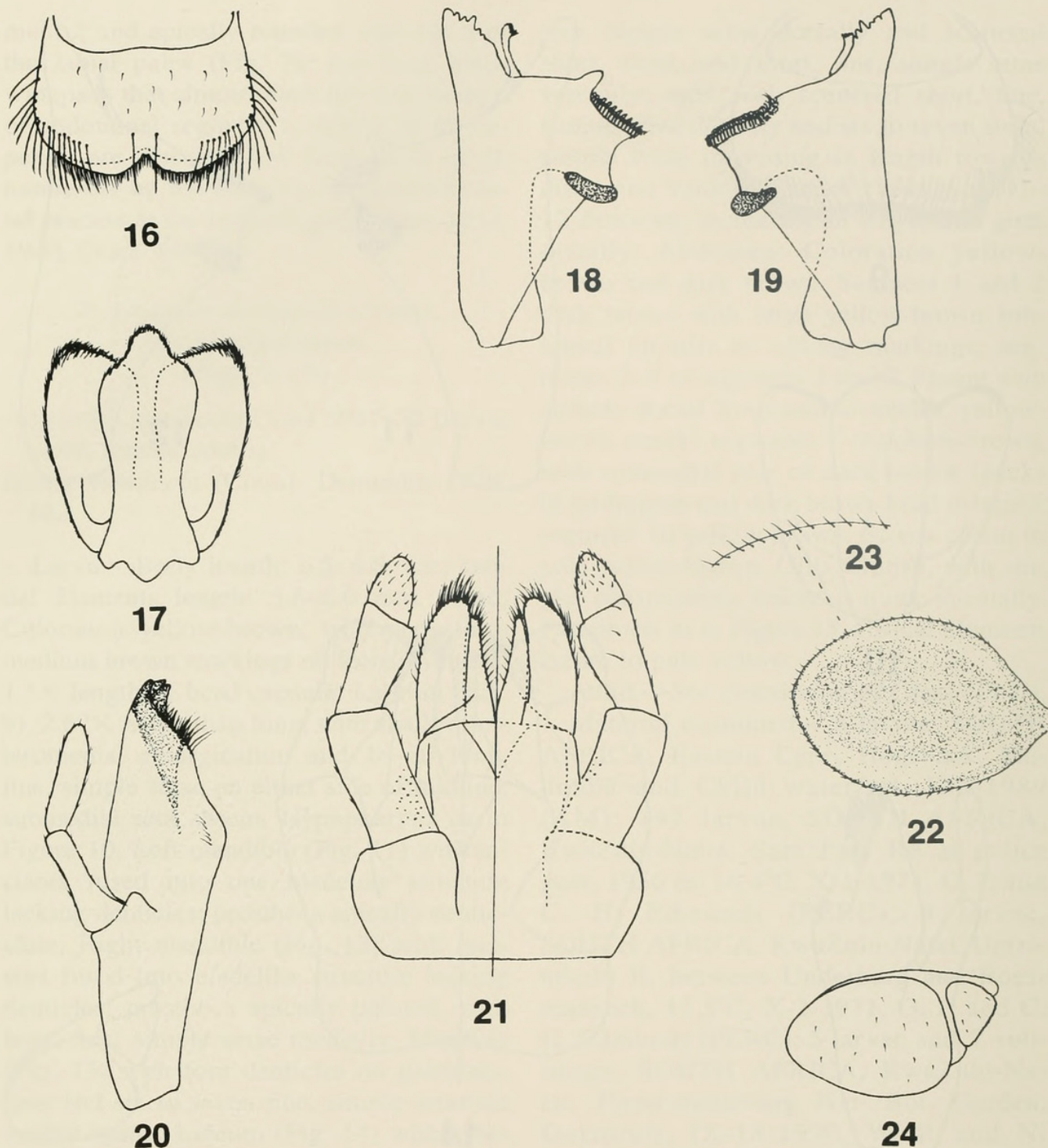
Figs. 9–15. *Demoreptus monticola*. 9, Labrum (dorsal). 10, Hypopharynx. 11, Left mandible. 12, Right mandible. 13, Right maxilla. 14, Labium (left-ventral; right-dorsal). 15, Paraproct.

bous segment 3 of the labial palps (Fig. 14). Adults of *D. monticola* differ from those of *D. capensis* in lacking an acute costal process in the hindwings, but evidently can only be told from those of *D. natalensis* by the presence of hindwings in both sexes (Crass 1947).

Demoreptus natalensis (Crass),
new combination
(Figs. 16–24)

Acentrella natalensis Crass 1947: 72 (larva; male, female adults).

Baetis natalensis (Crass): Demoulin 1970: 68.



Figs. 16–24. *Demoreptus natalensis*. 16, Labrum (dorsal). 17, Hypopharynx. 18, Left mandible. 19, Right mandible. 20, Right maxilla. 21, Labium (left-ventral; right-dorsal). 22, Gill 4. 23, Detail of gill margin. 24, Paraproct.

Larva.—Body length: 4.8–5.1 mm; caudal filaments length: 4.8–5.1 mm. Head: Coloration dark brown, with vermiform yellow-brown markings on frons. Antennae as long as head capsule. Labrum (Fig. 16) nearly $1.81\times$ wider than long, anteromedially deeply cleft, with submedial long, fine, simple seta and 10–11 long, fine, simple se-

tae on either side of midline. Hypopharynx as in Figure 17. Left mandible (Fig. 18) with six denticles; marginal lateral denticle small. Right mandible (Fig. 19) with six denticles; marginal lateral denticles small. Maxillae (Fig. 20) with four denticles on galealaciniae and five to six fine, simple setae on medial hump. Labium (Fig. 21) with

glossae subequal to paraglossae; paraglossae somewhat broad and long; palp segment 1 subequal to segments 2 and 3 combined; segment 2 with three to four fine, simple setae dorsally; palp segment 3 more or less pointed apically, not bulbous or clublike (width not exceeding that of apical width of segment 2). Thorax: Coloration dark brown, with irregular dark yellow-brown markings. Hindwingpads short, not more than $0.25 \times$ length of abdominal segment 1. Legs medium brown with irregular yellow-brown markings; femora with poorly developed villopore, row of long, robust, simple setae dorsally, and scattered short, stout and short, fine, simple setae ventrally; tibiae with row of short, fine, simple setae dorsally and scattered short, stout, and short, fine, simple setae ventrally; tarsi with row of short, fine, simple setae dorsally and eight to nine stout, simple setae increasing in length towards distal end ventrally; tarsal claws with 11–12 denticles, increasing in length and girth distally. Abdomen: Coloration dark brown to dark yellow-brown, with medium brown markings. Segment 1 dark yellow-brown, with dark brown anterior, posterior, and lateral margins; segment 2 dark brown, somewhat paler in midregion; segment 3 dark brown, with large sublateral dark yellow-brown quadrangles; segments 4 and 5 as segment 1, except with anterior submedial pair of small dark brown dashes; segments 6 and 7 as segment 1, except with submedial medium-sized dark brown circles in midregion; segments 8 and 9 as segments 6 and 7, except pale yellow-brown; segment 10 pale yellow-brown. Sterna pale yellow-brown to cream. Gills (Fig. 22) untracheated, dark yellow-brown to medium brown in midregion and whitish along margin; margin (Fig. 23) smooth and with fine, simple setae. Paraprocts as in Figure 24. Caudal filaments pale yellow-brown to cream.

Adult.—See description of Crass (1947).

Material examined.—7 larvae, LESOTHO, Schonghong R, Sangu-Orange Basin, Sani Rd bridge, IX-21-1988, P. H. Skelton

(AM); 2 larvae, SOUTH AFRICA, Eastern Cape, Berg R, at Hwy N2, nr Grahamstown, XI-13-1990, W. P. and N. McCafferty (PERC); 4 larvae, SOUTH AFRICA, Eastern Cape, Hogsback, Buffalo R, Madonna and Child waterfall, X-7-1989 (AM); 62 larvae, SOUTH AFRICA, KwaZulu-Natal, Sani Pass Rd at police post, 1950 m, 16.4°C , X-1-1971, G. F. and C. H. Edmunds (PERC); 5 larvae, SOUTH AFRICA, KwaZulu-Natal, Howick Falls, Umgeni R, 2-X-71, G. F. and C. H. Edmunds (PERC); 18 larvae, SOUTH AFRICA, KwaZulu-Natal, Impendle, W fork of Furth R, 1450 m, IX-18-1990, W. P. and N. McCafferty (PERC); larva, SOUTH AFRICA, KwaZulu-Natal, Impendle, Furth R, 1250 m, IX-18-1990, W. P. and N. McCafferty (PERC); 2 larvae, SOUTH AFRICA, KwaZulu-Natal, Camberg Nat. Res., riffle in Mooi R, IX-19-1990, W. P. and N. McCafferty (PERC); 36 larvae, SOUTH AFRICA, KwaZulu-Natal, Krantzloof Nat. Res., Molweni stream nr Kloof, 16.4°C , G. F. and C. H. Edmunds, X-4-1971 (PERC); 11 larvae, SOUTH AFRICA, KwaZulu-Natal, Molweni R at Krantzloof Nat. Res., 978 m, nr Durban, IX-21-1990, W. P. and N. McCafferty (PERC); 21 larvae, SOUTH AFRICA, Mpumalanga, MacMac R, above MacMac Falls, nr Graskop, 1820 m, W. P. and N. McCafferty (PERC); 3 larvae, SOUTH AFRICA, Mpumalanga, Long Tom St. For., upper Sabie R, X-26-1990, W. P. and N. McCafferty (PERC).

Discussion.—Larvae of *D. natalensis* are distinguished from those of *D. capensis* by the setation of the labrum (Fig. 16), small marginal incisors of the mandibles (Figs. 18, 19), the apically narrowly rounded labial palps (Fig. 21), and brown abdominal gills that are submarginally whitish (Fig. 22). Adults of *D. natalensis* can be separated from those of *D. capensis* by the absence of a costal process in the hindwings, and evidently can be separated from those of *D. monticola* by the absence of hindwings in its males (Crass 1947).

KEY TO THE LARVAE OF *DEMOREPTUS*

1. Labial palps segment 3 bulbous and clublike (medially broader than apical width of segment 2) (Fig. 14); labrum with shallow anteromedial emargination (Fig. 9); incisors of mandibles adenticulate and bladelike (Figs. 11, 12) . . .
D. monticola
- Labial palps segment 3 not bulbous, narrowly or broadly rounded apically (width not exceeding that of apical width of segment 2) (Figs. 7, 21); labrum anteromedially deeply cleft (Figs. 3, 16); incisors of mandibles with distinct denticulation (Figs. 4, 5, 18, 19) 2
2. Labial palps segment 3 narrowly rounded apically (Fig. 21); hindwingpads less than $0.25\times$ length of abdominal segment 1; abdominal gills brown, submarginally whitish (Fig. 22)
D. natalensis
- Labial palps segment 3 broadly rounded apically (Fig. 7); hindwingpads long, almost reaching hind margin of abdominal segment 1; abdominal gills whitish throughout . . .
D. capensis

INTERSPECIFIC RELATIONSHIPS

Using *Baetis* as our outgroup for cladistic analysis of species relationships within *Demoreptus*, we hypothesize that *D. capensis* is the most plesiotypic species, whereas *D. monticola* and *D. natalensis* represent sister species. Overall, however, *D. capensis* appears most similar to *D. natalensis*; both have anteriorly notched labra with a submedial pair of long, simple setae (Figs. 3, 16), denticulate mandibles (Figs. 4, 5, 18, 19), and well-demarcated labial palps with a segment 3 whose width does not exceed that of segment 2 (Figs. 7, 21). Those similarities, however, are based on symplesiomorphies, and therefore are not indicative of common ancestry between the two species. Furthermore, *D. monticola* is a highly evolved species and thus very distinctive. Nevertheless, we consider the loss of the costal process in the hindwings of *D. monticola* and *D. natalensis* (Crass 1947: Figs. 16b, 18b) a compelling synapomorphy indicative of the recent common ancestry of these species. *Demoreptus capensis* retains the plesiomorphic acute costal process (Barnard 1932: Fig. 12b) in the

hindwings, similar to that seen in *Baetis* and most other baetines.

Because, phenotypically, *D. monticola* is the most distinct of the three species and *D. capensis* and *D. natalensis* are most similar to each other, it would be tempting to erect a separate genus for *D. monticola*. However, it is not cladistically allowable because a separate taxon for *D. capensis* and *D. natalensis* would be paraphyletic. This situation is similar to that among the species of *Acanthiops*, where *A. marlieri* (De-moulin), being highly evolved, shows an extreme expression of clinal characters that may lead incorrectly to interpret it as a separate clade (see Barber-James and McCafferty 1997).

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