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The status of Cleptoria divergens (Chamberlin) (Polydesmida: Xystodesmidae)

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INTRODUCTION

In 1981 I revised the apheloriine xystodesmid genus *Sigmoria* and provided a homogeneous definition of the taxon. Key aspects of this diagnosis include: the sigmoid curvature of the acropodite, which passes through one or more vertical planes and forms an arch consisting of three regions—the "basal" and "distal zones" and the "peak"—and the presence of a medial flange on either the proximal portion of the peak or the proximal portion of the distal zone. The basal zone and peak are separated by the "anterior bend," and the acropodite usually exhibits an "apical curve" formed by the distal zone. Most of the "sigmoid" xystodesmids of the southern Blue Ridge Province conform to this description and are therefore encompassed by this concept of *Sigmoria*. The genus currently consists of 22 species, 3 of which are divided into a total of 9 subspecies.

There is, however, one other southern Appalachian "sigmoid" species that conforms to the *Sigmoria* gonopodal plan: *Cleptoria divergens* (Chamberlin). Hoffman (1967) transferred this species and *nigrescens* Hoffman from *Sigmoria* into *Cleptoria* and reduced *nigrescens* to subspecific status. I have previously stated (1981) that this action should be reviewed in light of the revised concept of *Sigmoria*. The species exhibits few similarities with the type of *Cleptoria, C. macra* Chamberlin, and seems just as out of place in that genus as *Brevigonus shelfordi* (Loomis) was before Hoffman (1967) removed it from *Cleptoria*. Two statements in Hoffman's paper suggested doubt about the desireability of bringing *divergens* into *Cleptoria*. First, he noted that the species "has a somewhat less characteristic gonopod and rather approximates a structure one might consider as fairly typical of *Sigmoria*." Then, he mentioned that all species of *Cleptoria* except *divergens* share a distinctive basic gonopod configuration.

Because of these ambiguities I conducted my own investigation into the systematic position of *divergens*, restudying all the material cited by Hoffman (1967) and collecting more in a thorough sampling of its range. I have concluded that the species is more compatible with the revised concept of *Sigmoria* than with *Cleptoria*, and that Chamberlin (1939) was correct in assigning *divergens* to this

genus. Moreover, I find no reason to recognize two geographic races and therefore assign *nigrescens* to synonymy under *divergens*. The species is anatomically unique and cannot be placed in any of the ten existing species groups of *Sigmoria;* consequently, its affinities are obscure and it must go into a group by itself, the third monotypic group in the genus. One minor change in the generic diagnosis is necessitated by the return of *divergens,* and I provide herein an updated range map (Fig. 6) of *Sigmoria.* This map also reflects the new record of *S. latior latior* (Brolemann) from Pulaski County, Virginia, which I obtained in time to report in an addendum to my 1981 paper but too late to include in the range map (Fig. 131).

LITERATURE REVIEW

Sigmoria divergens was proposed by Chamberlin (1939) from material supposedly taken at Landrum, Spartanburg County, South Carolina. As explained in the ensuing species account, Chamberlin confused specimens he had designated holotype and paratypes and so misreported the type locality in his original proposal. Recent authors, assuming Chamberlin was correct, repeated his error. Not only did Chamberlin confuse the type locality of *divergens,* but he also obscured the milliped's identity by mentioning nothing of taxonomic importance in the description and by failing to depict the complexity of the gonopods in his illustrations. Hoffman (1950a) included *divergens* in his summary of *Sigmoria* and (1950b) proposed *S. nigrescens* for a form from Sassafras Mountain, Pickens County, South Carolina. His description and illustrations in the latter paper established the identity of *nigrescens.* Chamberlin & Hoffman (1958) included both *divergens* and *nigrescens* in their listing of the North American diplopod fauna. In reducing *nigrescens* to a subspecies of *divergens,* Hoffman (1967) stated that the relationship between them was "subspecific at best," and he chose to recognize *nigrescens* mainly because of its different color. The nominate subspecies had red paranota and metatergal stripes, whereas *d. nigrescens* ranged from purple to black in these markings. He also alluded to a slight terminal difference in the gonopods of the two races, which was shown in illustrations but not described in the text. As part of the revision, Hoffman provided a detailed description and gonopod illustrations of *d. divergens,* but these were prepared from a male from Greenville County, South Carolina, instead of from a type specimen. The only other literature reference to either *divergens* or *nigrescens* (Shelley 1981) suggested a review of their systematic position in light of the revised concept of *Sigmoria.* I stated that they did not seem congeneric with the type of *Cleptoria* and should probably either be returned to *Sigmoria* or assigned to a new, monotypic genus.

Genus **Sigmoria** Chamberlin

Sigmoria Chamberlin, 1939:7. Hoffman, 1950a:1-2; 1980:158. Chamberlin and Hoffman, 1958:49. Shelley, 1981: 16-18.
Sigiria Chamberlin, 1939:9. Chamberlin and Hoffman, 1958:48.
Falloria Hoffman, 1948:93-94; 1979:159. Chamberlin and Hoffman, 1958:33.

Remarks: My definition of *Sigmoria* (1981) covers *divergens* rather well except that the distal zone in this species curves abruptly laterad from the peak instead of downward toward the prefemur. Consequently, it is not coplanar with the basal

zone or any other section of the acropodite and is obscured in medial view by the stem of the acropodite (Fig. 2). It can only be examined from the lateral perspective. Accordingly, the apical curve in *divergens* is very tight and narrow, much as in *S. stibarophalla* Shelley. The distal zone also bends laterad in *S. disjuncta* Shelley, but the thin acropodite of this species does not obscure it in medial view. This condition was treated as an individual specific trait of *disjuncta* in my revision, but it should now be incorporated into the generic diagnosis because it is seen in a second, unrelated species. Consequently, the description of the distal zone should be amended to read as follows: region forming apical curve (distal zone) varying in length, either projecting directly dorsad, curved inward into acropodite arch, or bent abruptly laterad, usually essentially coplanar with basal zone except when bent laterad, either of subequal width throughout most of length (except extreme tip) or tapering smoothly to acuminate tip.

The generalized generic range description that I presented (1981) must be slightly modified with admission of *divergens* to *Sigmoria* to include more of the eastern Blue Ridge Mountains along the North Carolina-South Carolina border. Some of this area was shaded in my earlier Fig. 131 (1981) because *S. latior munda* Chamberlin also occurs there, but it now must be enlarged slightly as shown in Fig. 6.

Species: With admission of *divergens*, *Sigmoria* now includes 23 species, three of which are divided into a total of nine subspecies. In my key to species (1981), *divergens* keys out at couplet 7 with *S. areolata* Shelley, since the distal zone does not project well into the arch of the acropodite.

The **Divergens** Group

The *divergens* group is the third monotypic group in *Sigmoria*, the others being the *bidens* and *tuberosa* groups, whose affinities are obscure. The abrupt lateral bend on the distal zone separates this group from all others, and it is also characterized by the apically expanded distal zone, the thickened, non-laminate flanges, and the proximal crossing of the prostatic groove from medial to lateral sides of the acropodite on the basal zone rather than at the anterior bend. The presence of a blunt apical tooth on the medial flange suggests distant affinity with the *latior* group; however, the *divergens* group does not share any significant features with the geographically proximate *stenogon* group.

Sigmoria divergens Chamberlin, revived combination. Figs. 1-5.

Sigmoria divergens Chamberlin, 1939:8, figs. 19-21. Hoffman, 1950a:4. Chamberlin and Hoffman, 1958:49.
Sigmoria nigrescens Hoffman, 1950b:28-29, figs. 28-32. Chamberlin and Hoffman, 1958:51. **New Synonymy**
Cleptoria divergens divergens: Hoffman, 1967:21-23, figs. 1, 17-19.
Cleptoria divergens nigrescens: Hoffman, 1967:23-25, fig. 20.

Type specimens: Male holotype (RVC) collected by R. V. Chamberlin, 5 August 1910, from Saluda, Polk Co., NC. Hoffman (1950a) and Chamberlin and Hoffman (1958) followed Chamberlin (1939) in reporting Landrum, Spartanburg Co., SC, as the type locality, but the label with the male from Saluda clearly indicates that this specimen is the holotype. Landrum is the locality of the female allotype and several male and female paratypes, which are also clearly labeled in the RVC collection. Chamberlin secured these specimens on 4 August 1910.

Diagnosis: A moderate-size species of *Sigmoria* with narrow medial flange on proximal portion of peak and with variable color pattern, paranota either red, purple, or dark gray, metaterga with concolorous transverse stripes along caudal margins; gonopods with following diagnostic characters: anterior bend sharp, well defined; medial flange thick, narrow, and poorly defined, extending most of length of peak, poorly demarcated from acropodite stem, with wide, rounded tooth apically; distal zone bent abruptly laterad from peak, not coplanar with basal zone, obscured in medial view by stem of acropodite, apically expanded; apical curve very tight and narrow, lateral flange distinct but thick, non-laminate.

Holotype: Although descriptions of this species were presented by Hoffman as *S. nigrescens* (1950b) and *C. d. divergens* (1967), respectively, the holotype has never been characterized. The 1967 description was of a male from Greenville Co., SC, which differs slightly from the holotype, particularly in the configuration of the prefemoral process.

Length 40.0 mm, maximum width 10.4 mm, W/L ratio 26.0%, depth/width ratio 61.5%. Segmental widths as follows:

collum	7.6 mm	12th-14th	10.0
2nd	8.0	15th	9.6
3rd	9.1	16th	9.0
4th-5th	9.9	17th	7.7
6th-9th	10.4	18th	5.4
10th-11th	10.2		

Color in life (Chamberlin 1939): paranota red; metaterga black with wide, red, trasverse stripes along caudal edges connecting paranotal spots; collum with red stripes along both anterior and caudal edges.

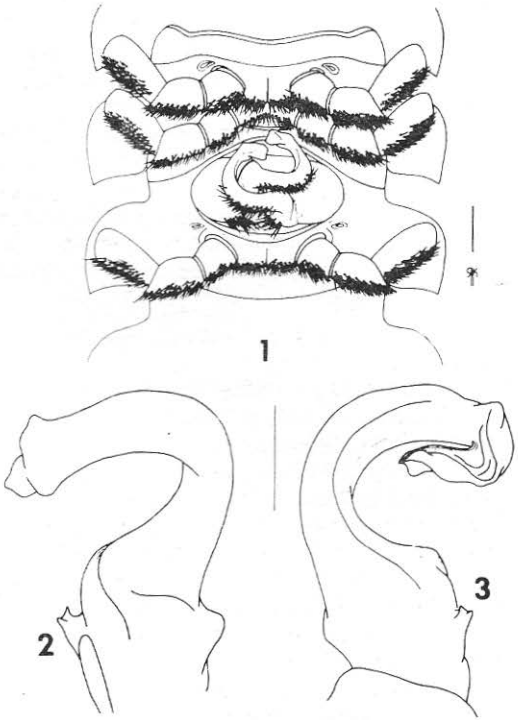
Head capsule smooth, polished; width across genal apices 4.6 mm; interantennal isthmus 1.6 mm; epicranial suture faint. Antennae relatively short, extending only to caudal margin of 2nd tergite, relative lengths of antennomeres 2>3>4=5=6>1>7, 2-6 clavate, 7 short and truncate. Genae not margined laterally, with distinct medial impressions, ends broadly rounded and extending slightly beyond adjacent cranial margins. Facial setae as follows: epicranial and interantennal absent, frontal 1-1, genal 1-1, clypeal about 12-12, labral about 18-18.

Terga smooth, polished, becoming moderately coriaceous on paranota. Collum moderate in size, extending slightly beyond ends of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 7, becoming blunt and progressively more pointed posteriorly. Peritremata sharp and distinct, sharply elevated from paranotal surface; ozopores located caudal to midpoint of peritremata, opening dorsad.

Sides of metazonites relatively smooth, with only slight impressions. Strictures distinct. Sternum of segment 4 with small, apically rounded process between 3rd legs, much shorter in length than widths of adjacent coxae (see Hoffman (1967), Fig. 1); of segment 5, with two small lobes between both pairs of legs; of segment 6, recessed between 7th legs to accommodate curvatures of acropodites, with dense tufts of setae between 6th and 7th legs. Postgonopodal sterna relatively flat, with transverse grooves between leg pairs and medial longitudinal grooves. Coxae with blunt tubercles beginning on legs of segment 9, becoming spiniform on segment 11 and continuing caudad; prefemoral spines sharply pointed; tarsal claws bisinuately curved. Hypoproct broadly rounded, paraprocts with margins strongly thickened.

Gonopodal aperture broadly ovoid, 3.4 mm wide and 1.8 mm long at midpoint, indented slightly along anterio-lateral margin, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 1, not this specimen) with acropodites extending

over opposite side of aperture, lying curved one inside other in midline, extending forward slightly beyond anterior margin of aperture. Gonopod structure as follows (Figs. 2-3): coxa moderate in size. Prefemur larger than in most species of *Sigmoria*, with short, blunt, apically bifurcate process arising on anterior side. Acropodite relatively thick and heavy, arch flattened at peak and extending slightly beyond level of prefemoral process, distal zone directed laterad from peak, not coplanar with basal zone; basal zone relatively long, with large lobe basally on outer margin; anterior bend sharp (about 90°), well defined, located at 1/3 length; peak relatively long and flattened, about 1/3 of acropodite length; apical curve sharp and very narrow, well defined; distal zone extending laterad from peak and directed toward anterior bend by narrow apical curve, obscured in medial view by stem of acropodite, apically expanded but sides tapering rapidly to simple, subacute tip. Medial flange narrow but thick and heavily sclerotized, poorly demarcated from stem of acropodite, arising at anterior bend, terminating proximal to apical curve in wide, rounded, fused tooth. Lateral flange thick and heavily sclerotized, arising at apical curve, indented slightly basally, then expanding into broadly rounded lobe and terminating proximal to tip. Prostatic groove arising in pit on prefemur, running along ridge on inner surface of acropodite, crossing to lateral side on basal zone proximal to anterior bend, terminating at tip of distal zone.



Figs. 1-3. *Sigmoria divergens*. 1, gonopods *in situ*, ventral view of male from 1.2 mi. NNE Saluda, Polk Co., NC. 2, telopodite of left gonopod of holotype, medial view. 3, the same, lateral view. Scale line for fig. 1 = 1.00 mm; line for other figs. = 1.00 mm for each.

Female Allotype: Length 46.1 mm, maximum width 10.7 mm, W/L ratio 23.2%, depth/width ratio 69.2%. Agreeing closely with male in somatic details except paranota more strongly depressed, angled sharply ventrad, creating appearance of more highly arched body.

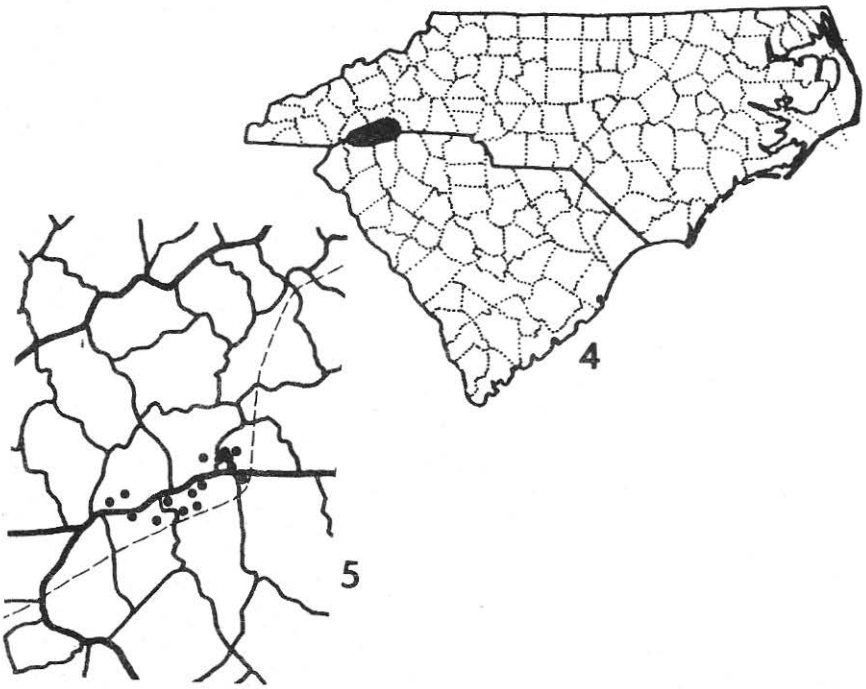
Cyphopods *in situ* with edge of receptacle visible in aperture, valves directed caudad. Receptacle very large, hood-like, almost completely enveloping valves, extending around ventral, lateral, and anterior sides of valves, surface rugulose. Valves moderate and subequal, surface finely granulate. Operculum minute, hidden under free (dorsal) end of valves.

Variation: Hoffman (1967) touched on variation in his diagnosis of *C. d. nigrescens*. The paranotal spots and metatergal stripes are darker in the southern half of the range and vary from gray to purple. The reddish color of specimens in the northern part (Henderson and Polk counties, North Carolina) is somewhat darker and takes on more of a maroon hue than the red markings of other "sigmoid" species in this general area, for example *stibarophalla*.

In my opinion the gonopods of *divergens* show little variation and are relatively constant, aside from insignificant differences in the configurations of the prefemoral processes and the arches of the acropodites. The prefemoral process is small in all males, but usually is not apically bifurcate as in the holotype. The slight differences in termination of the acropodite (distal zone) noted by Hoffman (1967) and illustrated in Figures 19-20 represent only a slightly smaller lateral flange in the form he labeled *C. d. nigrescens*. I cannot detect any significant variation in the lateral flange throughout the range of *divergens*, and this minor difference does not justify subspecific status, even when combined with the color differences. Other "sigmoid" species show color differences, for example *S. leucostriata* Shelley in which the paranota and stripes are light yellow in southern populations. Subspecies in these xystodesmids, however, should be based on gonopodal differences that can be shown to connect through intergrade specimens, as happens in the cases of *latior, S. rubromarginata* (Bollman), and *S. nigrimontis* (Chamberlin). Neither *divergens* nor *leucostriata* meets this criterion, and hence they are comprised of only one geographic race. *Sigmoria nigrescens*, therefore, becomes a synonym of *divergens*.

Ecology: Sigmoria divergens is a cove dwelling species (see Shelley (1981) for description for this habitat).

Distribution: An ovoid area in the eastern Blue Ridge Mountains and the Blue Ridge escarpment of North and South Carolina (Figs. 4-5), extending from about 5 miles NNE of Saluda to near the Horsepasture River. The area lies about equally in the two Carolinas and is bounded in the narrower dimension by US highway 64 in North Carolina and by state highway 11 (Cherokee Foothills Parkway) in South Carolina. The species has not been encountered in the Piedmont Plateau but it has spread nearly to the base of the escarpment. Nor does it occur at Pink Beds Recreation Area, 6-8 miles NNW of Brevard, Transylvania County, NC; the record from there by Hoffman (1967) is referrable to *S. stenogon* Chamberlin and included under the latter in my 1981 paper. However, *stenogon* and *divergens* are sympatric in Transylvania and Henderson counties, North Carolina, and their ranges overlap south of Brevard and Hendersonville. The two millipeds display similar color patterns in this area, and authentic determinations can be made only on mature males. The range of *divergens* also abuts those of two other "sigmoid" species of an undiagnosed genus in the Blue Ridge escarpment of Polk County north of Saluda. I have shown (1981), however, that *divergens* is not microsympatric with any of these species. Specimens were examined as follows; the collector's name is omitted for samples taken by the author alone, and the



Figs. 4-5. Distribution of *S. divergens*. 4, generalized range of *divergens* in North and South Carolina. 5, collection localities in eastern Blue Ridge Mountains. Dashed line is approximate boundary of southern Blue Ridge Province (Blue Ridge escarpment). Each dot marks a single collecting locality except the northernmost ones in Polk Co., NC, which represent several samples in the vicinity of Saluda and Tryon.

North Carolina State Museum (NCSM) invertebrate catalogue number is shown in parentheses by appropriate locality citations. Other collection acronyms are NMNH, National Museum of Natural History, Smithsonian Institution, Washington, DC; RLH, private collection of Richard L. Hoffman, Radford, VA; and RVC, private collection of the late Ralph V. Chamberlin, now being accessioned by the NMNH.

NORTH CAROLINA: *Polk Co.*, 4 mi. W Mill Spring, along co. rd. 1142, 1 mi. S jct. co. rd. 1170, M, 7 June 1978, R.M. Shelley and W.B. Jones (NCSM A2037); 1.6 mi. NE Saluda, along co. rd. 1151, 0.6 mi. N. jct. co. rd. 1142, 3 M, 3F, 14 July 1976 and 14 September 1977, (NCSM A1014, A1742); 3.7 mi. NE Saluda, along co. rd. 1151, 4.4 mi. N jct. co. rd. 1142, 11M, 6F, 14 July 1976 (NCSM A1015, A1016); 4 mi. NE Saluda, along co. rd. 1142 at Cove Cr., 2.4 mi. N. jct. co. rd. 1153, 5M, 2F, 14 July 1976 (NCSM A1020); 1.5 mi. E. Saluda, along co. rd. 1122, 0.7 mi. SE jct. co. rd. 1185, F, 7 June 1978, R.M. Shelley and W.B. Jones (NCSM A2038); Saluda, M, 5 August 1910, R.V. Chamberlin (RVC) TYPE LOCALITY; and Tryon, F, 7 June 1978, R.M. Shelley and W.B. Jones (NCSM A2040). *Henderson Co.*, 3.6 mi. SE Flat Rock, along US hwy. 176 at crossing of Green R., 2M, 3F, 8 June 1978, R.M. Shelley and W.B. Jones (NCSM A2047). *Transylvania Co.*, 4 mi. SW Rosman,

along co. rd. 1139, 0.8 mi. E jct. co rd. 1142, M, F, 11 September 1978, W.B. Jones (NCSM A2438); and ca. 4 mi. S Lake Toxaway, field camp of Highlands Biological Station in Horsepasture River Gorge, 5M, 2F, 16 July 1961, W.H. Adams and J.R. Paul (RLH).

SOUTH CAROLINA: *Spartanburg Co.*, Landrum, several MM and FF, 4 August 1910, R.V. Chamberlin (RVC). *Greenville Co.*, 1 mi. W Caesar's Head, 4M, 24 June 1950, L. Hubricht (RLH); 19.8 mi. N Travelers Rest, along SC hwy. 969, 1.3 mi. N jct. SC hwy. 17, M, 12 September 1978, W.B. Jones (NCSM A2441); along US hwy. 25, 1.5 mi. E NC line, M, 2F, 24 June 1950, L. Hubricht (RLH); Pleasant Ridge State Park, 4M, 12 August 1976 (NCSM A1400); and Wildcat Wayside State Park, M, 11 August 1976 (NCSM A1396). *Pickens Co.*, Table Rock State Park, 3M, 11 August 1976 (NCSM A1399); and south slope of Sassafras Mtn., 1 mi. W jct. US hwy. 178 and SC hwy. 288, 2M, F, 15 July 1949, R.L. Hoffman (NMNH, RLH).

Remarks: The following unique features of *divergens* justify its placement in a separate species group and render its affinities obscure: the abrupt lateral bend of the distal zone, which obscures it in medial view behind the stem of the acropodite and places it in a different vertical plane from the basal zone; the thickened, non-laminate medial and lateral flanges; the expanded distal zone; and the proximal crossing of the prostatic groove from medial to lateral sides of the acropodite.

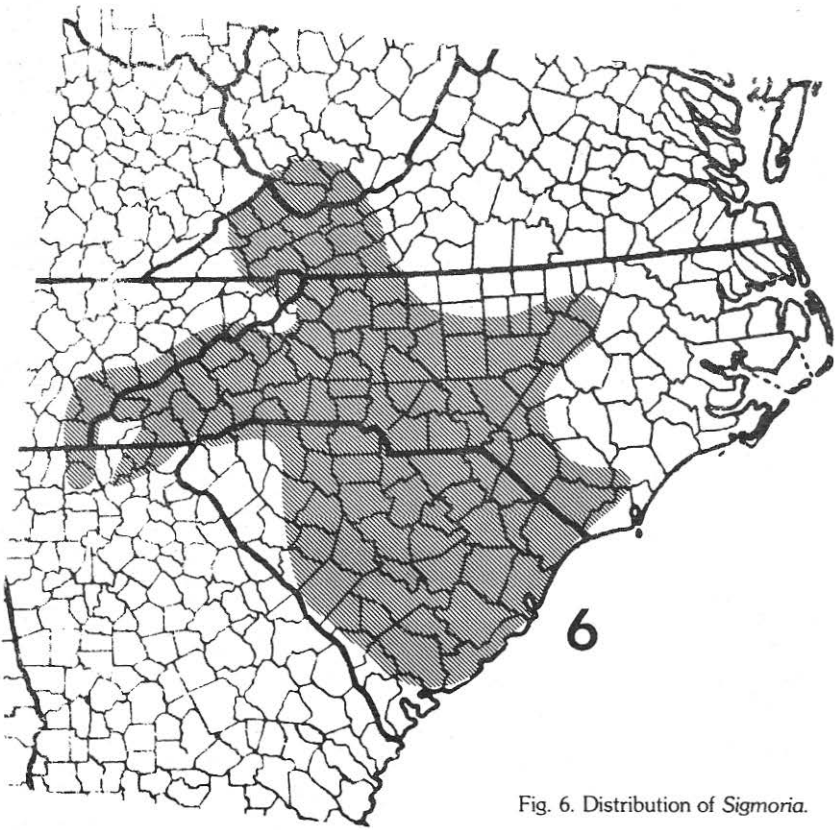


Fig. 6. Distribution of *Sigmoria*.

Certainly *divergens* has little in common with *stenogon*, with which it is sympatric in parts of Transylvania and Henderson counties, North Carolina. I intuitively feel that it is closest to *stibarophalla*, which occurs in Rutherford County near Lake Lure, not far from localities in Polk County inhabited by *divergens*. The narrow apical curve in *stibarophalla* is very similar to that of *divergens*, and the distal zone of the former is directed slightly laterad, although the acropodite of this species is so broad that it still lies mostly beneath the peak and can be considered coplanar with the basal zone. The distal zone of *stibarophalla* does not project as distinctly laterad as in *divergens*, but it is obscured in medial view in both species, by the enlarged medial flange in *stibarophalla* and by the stem of the acropodite in *divergens*. Affinity between *divergens* and *stibarophalla* is not as obvious as between many species of *Sigmoria*, but I believe it is the most plausible relationship for *divergens*.

I stated (1981) that *divergens* should either be returned to *Sigmoria* or placed in a new, monotypic genus. The latter option was quickly ruled out, however, after examination of material from throughout the range. The acropodites clearly conform to the basic *Sigmoria* pattern defined in 1981, and the proper systematic position of *divergens* is therefore as a species of *Sigmoria*.

ACKNOWLEDGMENTS

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