Paludicola 12(2): 46-52 June 2019

A LATE PLEISTOCENE RECORD OF *DRYMARCHON* SP. (SERPENTES: COLUBRIDAE: COLUBRINAE) FROM SOUTH CAROLINA, USA

James L. Knight[1,2,3] and David J. Cicimurri[4]

[1] Department of Biology and Geology, University of South Carolina Aiken, 476 University Parkway, Aiken, SC, 29201
[2] Research Associate, Florida Museum of Natural History, University of Florida, 3215 Hull Rd., Gainesville, FL, 32611
[3] Research Associate, Azuero Earth Project, Pedasi, Los Santos, Panama
<karin@gforcecable.com>
[4] South Carolina State Museum, 301 Gervais Street, Columbia, South Carolina 29801,
<dave.cicimurri@scmuseum.org>

ABSTRACT

Numerous isolated snake vertebrae within the late Pleistocene-aged Ardis Local Fauna from Dorchester County represent the first fossil record of the colubrid genus *Drymarchon* in South Carolina. Four measurements from each of fifty of these isolated vertebrae were used to statistically differentiate *Drymarchon* from morphologically similar vertebrae of *Coluber* and *Masticophis*. This study highlights the utility and necessity of standard measurements subjected to statistical methods to differentiate isolated fossil snake vertebrae. *Drymarchon* is not part of the extant South Carolina herpetofauna, and the fossil material therefore indicates that the geographic range of the genus has decreased slightly since the end of the last glacial maximum.

INTRODUCTION

Studies of squamate systematics and taxonomy have undergone a revolution over the past several decades. It is no longer sufficient to simply count scales and make notes on body coloration in order to discriminate between taxa. Phylogeography has opened new doors to understanding the relationships of extant, closely-related taxa and to recognizing cryptic taxa masquerading as other, similar forms. For example, within colubrid snakes *Drymarchon* is superficially very similar to *Masticophis* and/or *Coluber* (Meylan, 1982), particularly in their vertebral morphologies. Pyron et al. (2013) developed a phylogeny of Squamata using a "supermatrix approach" that included a combined total of 4161 taxa. The matrix contained 1262 snake species, which accounted for 39% of total snake diversity known at the time. Figueroa et al. (2016) reported on 1652 snake species, or 46.3% of total snake diversity, and both their study and that of Pyron et al. (2013) nested *Drymarchon* within the colubrid subfamily Colubrinae. Additionally, Figueroa et al. (2016) placed *Masticophis* in the genus *Coluber*, with varying degrees of taxonomic support.

Phylogenetic approaches have constraints, however, as fossils do not yield analyzable chemicals as often as researchers would like. Consequently, other, more tangible criteria must be utilized in order to ascertain placement of a particular specimen in one taxon or another.

The colubrid genus *Drymarchon* (indigo snakes) currently occupies a considerable range in the Western Hemisphere. This rather large taxon is known from southeastern Georgia and all of peninsular Florida, south and west along the U.S. Gulf Coast, to southeastern Mississippi (Gibbons and Dorcas, 2005; Stevenson et al., 2008; Powell et al., 2016). A large distributional gap occurs throughout the lower Mississippi River Valley and westward along the Texas gulf coast, but the genus is found from southern Texas and western Mexico southward to Paraguay and northern Argentina (Wallach et al., 2014). Once regarded as a single variable species (do Amaral, 1930), variation within *Drymarchon* has been reevaluated over the past several decades, and several species are now recognized (Wallach et al., 2014).

The eastern indigo snake, formerly the subspecies *Drymarchon corais couperi*, was elevated to full species status (=*D. couperi*) by Collins (1991), who based his decision on its allopatric distribution from congenerics. Although Ditmars (1939) reported the range of *D. couperi* to include southern North Carolina, and Ernst and Barbour (1989) showed the species ranging into southern South Carolina, the species is not currently recognized as part of the state's extant herpetofauna. The reported distribution of the species extends from south of the Savannah River in

Effingham County, Georgia, southward throughout Florida and westward to extreme southeastern Mississippi (Gibbons and Dorcas, 2005; Stevenson et al. 2008; Powell et al., 2016; Guyer et al., 2019). In the fossil record, indigo snakes are known from the Pleistocene of Florida and Alabama (Holman, 1995; Dobie et al., 1996).

The South Carolina State Museum has excavated several Pleistocene-aged vertebrate faunas from various locations on the middle and lower coastal plain of South Carolina. One such fauna, the Ardis Local Fauna (LF), was collected from sand- and clay-filled solution cavities occurring within an active limestone quarry in Dorchester County, South Carolina (Figure 1). Herein we document a late Pleistocene occurrence of *Drymarchon* in South Carolina, which represents the first record, fossil or Recent, of the genus in the state. The taxon is yet another extralimital taxon within the Ardis LF, and provides further support for a "disharmonious fauna" in South Carolina during the terminal Pleistocene.

GEOLOGIC SETTING AND AGE

The site yielding the Ardis LF occurred in the Giant Portland Cement quarry, located approximately four kilometers north of Harleyville, Dorchester County, South Carolina (Figure 1). The Ardis LF was collected from sand and clay infillings within solution cavities occurring at the top of the Late Eocene Tupelo Bay Formation (Bentley and Knight, 1993; Geisler et al., 2005). Groundwater chemically eroded less indurated portions of the limestone, and cavities of various sizes, some exceeding 1.5 m greatest dimension, had formed. Some of the cavities were open to the surface through holes from 4-15 cm in diameter, through which flood events washed sand and clay into them. Sediment cones formed under the openings, some of which were composed solely of sand and others consisting of alternating layers of sand and clay. These latter occurrences likely document the initial stronger flow and high sediment load of the flood, with later pooling and settling of finer sediment. Eventually sediment completely filled the cavities and closed off the space to the outside. The bones of birds and larger mammals like *Equus* sp. and *Megalonyx* sp. were either washed into the cavities (Bentley et al., 1994; Chandler and Bentley, 2007) or were carried there by other animals (Bentley and Knight, 1994). However, the cavities were large enough to allow smaller vertebrate species to pass into and out of them, and possibly use them as retreats. Some individuals, particularly turtles, died in life positions with their limbs pulled into their shells, likely buried alive (Bentley and Knight, 1993, 1998).

The mammalian species comprising the Ardis LF indicate a late Rancholabrean age, and ^{14}C dating of preserved collagen yielded an age range of 18,940 (±760 years) to 18,530 years (±725) (Bentley et al., 1994). This age coincides with the last glacial maximum, a time when cooler summers and warmer winters occurred in the area (Bentley et al., 1994).

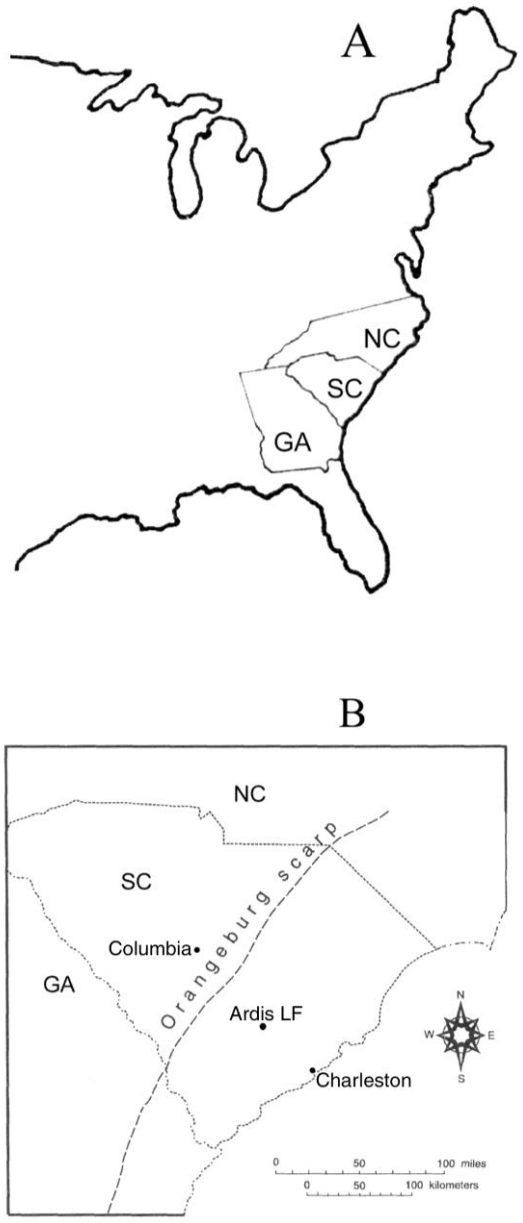

FIGURE 1: A, geographic map of the eastern United States showing locations of some southeastern coastal states. B, geographic map of South Carolina showing location of the Ardis Local Fauna site in Dorchester County, South Carolina. The Orangeburg Scarp is a wave-cut bank that formed during the Pliocene Epoch. Modified from Knight and Cicimurri (2010).

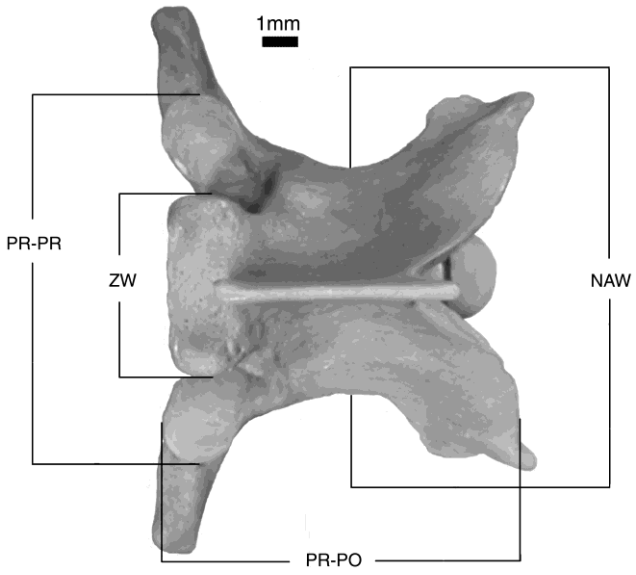

FIGURE 2: Dorsal view of *Drymarchon* vertebra (SC2019.1.7) from the Ardis Local Fauna, Dorchester County, South Carolina. Abbreviations: NAW=neural arch width; PR-PR=prezygopophysis width; PR-PO=pre- to postzygopophysis length; ZW=zygosphene width. Anterior is at left.

METHODS

Among the many thousands of snake vertebrae and skull elements represented in the Ardis LF are a number of vertebrae from a rather large colubrid snake. Fifty of these vertebrae, of various centrum lengths, were selected for their shape and completeness, and these are curated under SC2019.1.1–.50 at the South Carolina State Museum, Columbia. Four individual measurements were taken from each vertebra, including pre- to postzygopophysis length, prezygopophys width, zygosphene width, and neural arch width (see Figure 2). Measurements were taken with dial calipers and ratios were computed to one standard deviation of the mean to facilitate direct comparison with values published by Meylan (1982: table 4), who utilized Discriminate Function Analysis to compare various ratios of the vertebrae of the snake genera *Coluber*, *Masticophis* and *Drymarchon*. The measurement data for the 50 Ardis LF colubrid vertebrae are included in Appendix 1, and the results of our analysis of these vertebrae compared to the values obtained by Meylan are presented in Table 1.

DISCUSSION

With the description of *Drymarchon kolpobasileus* Krysko, Granatosky, Nuñez, and Smith, 2016, the so-called Gulf Coast indigo snake, two extant species of indigo snakes may occur in the southeastern United States. The validity of this species has been refuted (Folt et al., 2019), and Guyer et al. (2019) did not recognize the species in Alabama. On geographic grounds the Ardis LF vertebrae would be assigned to the nearest occurring extant taxon, *Drymarchon couperi*. However, without an analysis of the vertebral morphology of *Drymarchon*, it seems premature to assign an extralimital occurrence of a member of the genus to species, so we are allocating the Ardis LF vertebrae only to *Drymarchon* sp.

Holman (2000) stated that "Florida specimens have a distinctive neural spine that is slightly longer than high, overhangs posteriorly, and has a beveled anterior edge…," and he illustrated a vertebra (fig. 96, p. 156) of a Recent specimen exhibiting a pronounced bevel on the anterior edge of the neural spine. Meylan (1982) observed that his fossil specimens showed greater similarity to Mexican and Central American populations than to Florida populations, positing that differentiation of vertebral morphology in *Drymarchon* had occurred after the early Pleistocene, and suggesting that Florida populations were isolated from those north and west after the Irvingtonian North American Land Mammal Age (NALMA). The Ardis LF specimens, although considerably younger, are more similar to Meylan's (1982) description. Considerable variation exists in the neural spine shape within the Ardis LF sample, and this variation may represent the transition from "typical" neural spine shape to that seen in modern indigo snakes. Observation of many additional specimens will be necessary to understand the significance, if any, of this morphology. Additionally, appraisal of the skeletal morphology of southeastern US *Drymarchon* will be necessary to make a more accurate determination of the Ardis LF species.

Even though both *Coluber* and *Masticophis* (=*Coluber* sensu lato) are common components of the modern South Carolina herpetofauna, there are no valid recent or fossil records of *Drymarchon* from the state. Comparison of the results of our analysis of the Ardis LF fossil vertebrae to Meylan's (1982) data, which statistically distinguishes *Drymarchon* from *Coluber* and *Masticophis* (=*Coluber* sensu lato), clearly demonstrates the presence of indigo snakes in South Carolina's Ardis LF. The Ardis site is located approximately 110 km northeast of the northeastern-most record of *Drymarchon* in Georgia (Stevenson et al.,2008).

TABLE 1. Comparison of the results of statistical analyses of fossil and Recent colubrid snake vertebrae of Meylan (1982) with values we derived from the Ardis Local Fauna sample. Mean values are ± one standard deviation. Abbreviations for vertebral features follows Figure 2; n=number of specimens examined; LF=Local Fauna. Asterisk indicates apparent typographical error in standard deviation presented by Meylan (1982).

Taxon	ZW/NAW	PR-PR/PO-PR	PR-PR/NAW	PR-PR/ZW
Coluber constrictor				
recent (n=27)	0.98 ±0.04	1.04 ±0.04	1.79 ±0.10	1.83 ±0.11
fossil (n=334)	0.96 ±0.98*	0.99 ±0.05	1.74 ±0.11	1.90 ±0.15
Masticophis flagellum				
recent (n=26)	0.98 ±0.05	0.98 ±0.05	1.81 ±0.05	1.84 ±0.11
fossil (n=331)	0.95 ±0.08	0.97 ±0.05	1.80 ±0.11	1.89 ±0.13
Drymarchon corais				
recent (n=14)	0.81 ±0.02	1.12 ±0.06	1.65 ±0.07	2.03 ±0.06
fossil (n=29)	0.84 ±0.03	1.03 ±0.06	1.72 ±0.06	2.04 ±0.06
South Carolina Ardis LF				
fossil (n=50)	0.82 ±0.05	1.11 ±0.11	1.71 ±0.08	2.09 ±0.01

The presence of several extralimital taxa within the Ardis Local Fauna suggests very different environmental conditions at the time of deposition from that in existence in the region today. In addition to *Drymarchon*, Ardis LF species like *Spermophilus tridecemlineatus* (thirteen-lined ground squirrel), *Emydoidea blandingi* (Blanding's turtle) and *Tympanuchus* sp. (prairie grouse) are not part of the extant fauna of South Carolina. *Glyptemys muhlenbergii* (Muhlenberg's turtle) occurs in South Carolina only as a relict population in Spartanburg County. Additionally, *Chrysemys picta* (painted turtle) is primarily known from South Carolina only in the Piedmont and mountainous western portion of the state (Bentley et al., 1994; Bentley and Knight, 1998; Chandler and Bentley, 2007), both well to the northwest of the Ardis LF site. However, *C. picta* occurs rarely on the upper edge of the coastal plain, as Tuberville et al. (1996) reported capturing five migrant males on the Savannah River Site (Aiken County) over a 26 year period.

It should, perhaps, be no surprise that snakes of the genus *Drymarchon* are recognized from a paleofauna, demonstrating their past occurrence in South Carolina. Interestingly, the absolute age range obtained from turtle and mammal bone collagen indicates that the Ardis LF existed during the time of the southernmost advance of the Wisconsinan ice sheet of the Rancholabrean NALMA. Thus, an unusual environment of cooler summers and warmer winters allowed for the mixing of several otherwise distinct faunas, and the Ardis LF therefore provides an example of a "Disharmonious Community" (Lundelius et al.,1983; Holman, 1995).

CONCLUSIONS

Morphometrics are uncommonly used in paleo-herpetological analyses. Our study highlights the utility of statistical comparisons to identify fossil taxa. Our analysis of the Ardis Local Fauna vertebrae indicates that the specimens compare most favorably to recent and fossil *Drymarchon* (see Table 1), as opposed to the morphologically similar *Coluber* and *Masticophis*. As there is considerable debate regarding the validity of some extant species of *Drymarchon*, we refrain from making a more precise determination for the Ardis LF species based only on isolated vertebrae. However, the presence of the genus in the Ardis LF provides additional support for the hypothesis of disharmonious communities (Lundelius, 1983; Khenzykhenova, 1996), including in coastal South Carolina, at the end of the Pleistocene.

ACKNOWLEDGENTS

The authors wish to thank Burt Ardis of Giant Portland Cement for arranging access to the quarry and for numerous other kindnesses. Curtis Bentley and Vance McCollum originally recognized the significance of the site, and they and Linda Eberle worked tirelessly to collect the fossil fauna contained within. The editorial suggestions provided by Drs. Judy Massare (Paludicola), J. Whitfield Gibbons (Savannah River Ecology Lab, Aiken, SC) and Steve Fields

(Museum of York County, Rock Hill, SC) improved upon an earlier version of this manuscript and are greatly appreciated.

LITERATURE CITED

do Amaral, A. 1930. Estudios sobre ophídios neotrópicos. XXI. Revisao do genero *Drymarchon* Fitzinger, 1843. Memórias do Instituto Butantan (1929) 4:323−330.

Bentley, C.C., and J.L. Knight. 1993. The Oldest Spotted Turtle: *Clemmys guttata* (Testudines: Emydidae) from the Late Pleistocene (Rancholabrean) Ardis Local Fauna, Dorchester County, South Carolina. South Carolina Geology 36:59−63.

Bentley, C.C., and J.L. Knight. 1994. Comments on the Body Mass Trend of *Ondatra zibethicus* (Rodentia: Muridae) During the Latest Pleistocene. Brimleyana 21:37−43.

Bentley, C.C., and J.L. Knight. 1998. Turtles of the Ardis Local Fauna. Brimleyana 25:1−33.

Bentley, C.C., J.L. Knight, and M.A. Knoll. 1994. Mammals of the Ardis Local Fauna (Late Pleistocene), Harleyville, South Carolina. Brimleyana 21:1−35.

Chandler, R.M., and C.C. Bentley. 2007. Birds of the Ardis Local Fauna, Late Pleistocene, South Carolina. Current Research in the Pleistocene 24:162−163.

Collins, J.T. 1991. Viewpoint: a new taxonomic arrangement for some North American amphibians and reptiles. Herpetological Review 22:42−43.

Ditmars, R.L. 1939. A Field Book of North American Snakes. Doubleday and Company, Inc., Garden City, New York, New York, 305 pp.

Dobie, J.L., C.J. Leary, and J.A. Holman. 1996. A Pleistocene indigo snake, *Drymarchon corais*, from Bogue Chitto Creek, Dallas County, Alabama. Journal of the Alabama Academy of Science 67(1):1−3.

Ernst, C.H., and R.W. Barbour. 1989. Snakes of Eastern North America. George Mason University Press, Fairfax, Virginia, 282 pp.

Figueroa, A., A.D. McKelvy, L.L. Grismer, C.D. Bell, and S.P. Lailvaux. 2016. A species-level phylogeny of extant snakes with description of a new colubrid subfamily and genus. PLoS ONE, https://doi.org/10.1371/journal.pone.0161070.

Folt, B. J. Bauder, S. Spear, D. Stevenson, M. Hoffman, J.R. Oaks, P.L. Wood, Jr., C. Jenkins, D.A. Steen, and C. Guyer. 2019. Taxonomic and conservation implications of population genetic admixture, mito-nuclear discordance, and male-biased dispersal of a large endangered snake, *Drymarchon couperi*. PLoS ONE, https://doi.org/10.1371/journal.pone.0214439.

Geisler, J.H., A.E. Sanders, and X. Lou. 2005. A new protocetid whale (Cetacea: Archaeoceti) from the Late Middle Eocene of South Carolina. American Museum Novitates 3840:1−65.

Gibbons, J.W., and Dorcas, M.E. 2005. Snakes of the Southeast. The University of Georgia Press, Athens, 253 pp.

Guyer, C, M.A. Bailey, and R.H. Mount. 2019. Lizards and Snakes of Alabama. University of Alabama Press, Tuscaloosa, 416 pp.

Holman, J.A. 1995. Pleistocene Amphibians and Reptiles in North America. Oxford University Press, New York, New York, 256 pp.

Holman, J.A. 2000. Fossil Snakes of North America: Origin, Evolution, Distribution, Paleoecology. Indiana University Press, Bloomington, 237 pp.

Khenzykhenova, F. 1996. Late Pleistocene small mammals from the Baikal region (Russia). Acta Zoologica Cracoviensia 39(1):229−234.

Knight, J.L., and D.J. Cicimurri. 2010. First report of fossil *Amphiuma* (Amphibia: Caudata: Amphiumidae) from South Carolina, USA. Paludicola 8(1):1−7.

Krysko, K.L., M.C, Granatosky,L.P. Nuñez, and D.J. Smith. 2016. A cryptic new species of Indigo Snake (genus *Drymarchon*) from the Florida Platform of the United States. Zootaxa 4138 (3):549−569.

Lundelius, E.L. 1983. Climatic implications of Late Pleistocene and Holocene faunal associations in Australia. Alcheringa: An Australasian Journal of Palaeontology 7(2):125−149.

Lundelius, E.L., R.W. Graham, E. Anderson, J. Guilday, J.A. Holman, D.W. Steadman, and S.D. AmWebb. 1983. Terrestrial vertebrate faunas; pp. 311− 353 in H. E. Wright (ed.), Late Quaternary Environments of the United States. Vol. 1: The Late Pleistocene. University of Minnesota Press, Minneapolis.

Meylan, P. 1982. The squamate reptiles of the Inglis 1A fauna (Irvingtonian: Citrus County, Florida). Bulletin of the Florida State Museum 27:1−85.

Powell, R., R. Conant, and J.T. Collins. 2016. Peterson Field Guide to Reptiles and Amphibians of Eastern and Central North America. 4th Ed. Houghton Mifflin Harcourt Publishing Company, New York, New York, 509 pp.

Pyron, R.A., F.T. Burbrink, and J.J. Weins. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC 13, 93 pp.

Stevenson, D.J., R.A. Moulis, and N.L. Hyslop. 2008. Eastern Indigo Snake: *Drymarchon couperi*; pp. 339−341 in J.B. Jensen, C.D. Camp, W. Gibbons,

and M.J. Elliott (eds.), Amphibians and Reptiles of Georgia. University of Georgia Press, Athens.

Tuberville, T.D., J.W. Gibbons, and J.L. Greene. 1996. Invasion of new aquatic habitats by male freshwater turtles. Copeia, 1996(3):713−715.

Wallach, V., K.L. Williams, and J. Boundy. 2014. Snakes of the Word: A Catalogue of Living and Extinct Species. CRC Press, Taylor and Francis Group, Boca Raton, Florida, 1209 pp.

APPENDIX 1

Measurement data (in millimeters) for the 50 Ardis LF colubrid vertebrae examined. Abbreviations follow Figure 2.

Catalogue #	ZW	PR-PR	PR-PO	NAW
SC2019.1.1	4.75	5.65	9.95	8.90
SC2019.1.2	4.70	5.85	10.40	9.20
SC2019.1.3	4.60	5.65	9.70	9.05
SC2019.1.4	4.90	6.55	11.75	10.40
SC2019.1.5	5.80	7.85	12.85	12.35
SC2019.1.6	4.90	6.05	10.15	9.40
SC2019.1.7	5.45	6.95	11.20	10.25
SC2019.1.8	4.05	4.65	8.85	8.20
SC2019.1.9	5.65	6.90	11.35	10.15
SC2019.1.10	5.15	6.35	10.95	10.25
SC2019.1.11	4.65	5.55	9.45	8.80
SC2019.1.12	4.30	4.85	8.30	7.80
SC2019.1.13	5.00	5.85	9.95	9.15
SC2019.1.14	5.45	7.00	11.10	10.20
SC2019.1.15	4.25	5.10	9.30	8.70
SC2019.1.16	4.40	5.65	8.90	8.10
SC2019.1.17	5.30	6.90	10.85	9.90
SC2019.1.18	4.25	5.10	8.40	7.85
SC2019.1.19	5.20	6.35	10.70	9.75
SC2019.1.20	6.00	7.30	12.60	7.05
SC2019.1.21	5.05	6.70	10.65	9.80
SC2019.1.22	4.30	6.15	9.95	8.70
SC2019.1.23	5.20	6.45	11.50	9.75
SC2019.1.24	5.15	6.70	11.20	9.65
SC2019.1.25	5.45	6.30	11.05	9.30
SC2019.1.26	4.40	5.15	8.70	8.70
SC2019.1.27	4.65	5.20	9.45	9.10
SC2019.1.28	5.20	6.55	10.75	10.05
SC2019.1.29	5.70	6.65	10.70	10.30
SC2019.1.30	4.50	5.20	9.30	8.30
SC2019.1.31	4.05	4.80	8.75	8.05
SC2019.1.32	4.95	5.75	9.55	9.50
SC2019.1.33	4.25	5.20	8.95	8.10
SC2019.1.34	4.95	5.50	9.80	9.15
SC2019.1.35	5.40	6.25	10.90	9.75
SC2019.1.36	4.60	5.40	9.25	8.10
SC2019.1.37	5.30	6.45	10.45	9.80
SC2019.1.38	4.55	5.35	9.50	8.85
SC2019.1.39	4.20	5.05	8.60	8.35
SC2019.1.40	5.00	6.15	9.85	8.85
SC2019.1.41	4.70	5.85	9.55	8.75
SC2019.1.42	4.05	5.35	9.40	8.85
SC2019.1.43	5.45	6.20	10.95	9.55
SC2019.1.44	4.95	6.65	11.05	9.60
SC2019.1.45	4.45	5.55	9.40	8.55
SC2019.1.46	4.30	5.30	9.15	8.45
SC2019.1.47	4.30	5.55	9.35	8.45
SC2019.1.48	4.80	5.50	9.40	9.10
SC2019.1.49	4.20	5.60	10.05	8.50
SC2019.1.50	4.45	5.75	10.40	9.40