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A Review of the Fossil Record of Turtles of the Clade *Pan-Chelydridae*

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ABSTRACT

Turtles of the total clade *Pan-Chelydridae* have a relatively sparse fossil record that reaches back to the Late Cretaceous (Santonian). The clade was only present in North America during the Cretaceous but spread along unclear routes to Asia and Europe during the Paleocene, only to go extinct on those continents by the end of the Pliocene. Final dispersal to South America took place at some time during the late Neogene. The ecology of stem chelydrids seems to have been similar to that of the extant *Chelydra serpentina*, although more primitive representatives were more molluscivorous as inferred from their broader triturating surfaces. Current phylogenies only recognize five internested clades: *Pan-Chelydridae*, *Chelydridae, Chelydropsis, Chelydra* and *Macrochelys*. A taxonomic review of the group concludes that of 31 named fossil taxa, 8 are nomina valida, 10 are nomina invalida, 9 are nomina dubia, 1 is a nomen nudum and 1 is a regular, unavailable name.

KEYWORDS

Phylogeny, Biogeography, Paleoecology, *Pan-Chelydridae, Chelydridae, Chelydropsis*

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Introduction

The term *Pan-Chelydridae* refers to the total clade of *Chelydridae*, which is the crown clade arising from the most recent common ancestor of the common snapping turtle *Chelydra serpentina* (Linnaeus, 1758) and the alligator snapping turtle *Macrochelys temminckii* (Troost in Harlan, 1835). Historically, chelydrids (i.e., snapping turtles) were recognized to have close relationships with kinosternoids (i.e., mud and musk turtles), mostly based on characters derived from the shell, such as the presence of costiform processes and a cruciform plastron (e.g., Gray 1869; Boulenger 1889; Baur 1893; Siebenrock 1909; Williams 1950; Romer 1956; Kuhn 1964; Sukhanov 1964; Młynarski 1976; Carroll 1988), but early classifications often failed to include important taxa in this grouping, particularly the Central American river turtle *Dermatemys mawii* Gray, 1847, or wrongfully included others, such as the aberrant Asian big-headed turtle *Platysternon megacephalum* Gray, 1831.

With the advent of cladistic methods, Gaffney (1975a, 1975b) suggested that cranial characters link chelydrids with testudinoid turtles and that *Platysternon megacephalum* should be regarded as a true snapping turtle. Subsequent cladistic analyses supported the distinct nature of pan-chelydrids and placed this clade as sister either to all other extant cryptodires (e.g., Gaffney et al. 1991; Hirayama et al. 2000; Tong et al. 2009) or to testudinoids and trionychoids (e.g., Brinkman and Wu 1999; Joyce 2007). A series of increasingly well-sampled analyses that utilize molecular data (e.g., Shaffer et al. 1997; Krenz et al. 2005; Parham et al. 2006; Barley et al. 2010; Crawford et al. 2015), however, have more recently revived the sister group relationship between chelydrids and kinosternoids to the exclusion of *P. megacephalum*. This resulting "superfamilial" clade is named *Chelydroidea* following Baur (1893), who was the first to recognize this exact arrangement (Knauss et al. 2011). Although current morphological studies still fail to retrieve a monophyletic *Chelydroidea* (e.g., Joyce 2007; Anquetin 2012; Sterli et al. 2013; Rabi et al. 2014), some compelling character evidence is nevertheless available that supports the monophyly of this clade (Knauss et al. 2011).

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Throughout the 19th century, fossil pan-chelydrids were only known from Oligocene to Pliocene deposits in Germany (Bell 1836; Meyer 1845, 1852; Winkler 1869; Fraas 1870) and Austria (Peters 1855, 1868, 1869; Gross 2002), far outside the current distribution of the clade in North and South America; however, their attribution to *Pan-Chelydridae* was always unambiguous, as these finds include complete skeletons that clearly reveal their phylogenetic affinities. The European fossil record was only later supplemented by mostly fragmentary finds from the Czech Republic (Laube 1900, 1910), France (Broin 1977), Kazakhstan (Chkhikvadze 1971, 1973), Moldova (Khosatzky and Redkozubov 1989), Poland (Młynarski 1981a, 1981b), Romania (Młynarski 1966, 1969), Slovakia (Młynarski 1963; Danilov et al. 2012), Spain (Murelaga et al. 1999; Murelaga et al. 2002), Ukraine (Pidoplichko and Tarashchuk 1960; Tarashchuk 1971), and Turkey (Paicheler et al. 1978). Additional fossil material has been reported from Georgia and Russia (see Syromyatnikova et al. 2013 for a summary); however, none has been figured, and it is therefore not possible to reproduce these reports.

The fossil record of North American pan-chelydrids remained elusive throughout the 19th century (Hay 1908b). Some well-preserved skulls were finally described in the mid-20th century from Neogene sediments (e.g., Matthew 1924; Zangerl 1945; Dobie 1968; Whetstone 1978a), and their attribution to crown *Chelydridae*, in particular the *Macrochelys* lineage, was uncontroversial once again, as these beautifully preserved fossils clearly revealed many unambiguous apomorphies. The Neogene record has since only been supplemented by fragmentary postcranial remains with less certain phylogenetic affiliations. Relatively rich remains of more basal pan-chelydrids have otherwise been retrieved more recently from Late Cretaceous (Campanian) to Paleocene sediments throughout western North America, in particular the Santonian and Campanian of Alberta, Canada (Brinkman 2003; Brinkman and Eberth 2006); the Campanian of Mexico (Rodriguez-de la Rosa and Cevallos-Ferriz 1998) and Utah, USA (Hutchison et al. 2013); and the Maastrichtian to Paleocene of Montana, North Dakota and Wyoming, USA (Erickson 1973, 1982, 1984, 2010; Hutchison and Archibald 1986; Holroyd and Hutchison 2002; Hutchison 2013; Holroyd et al. 2014).

Given that pan-chelydrids and pan-kinosternoids originate from a common ancestor, it is sometimes difficult to rigorously distinguish early representatives of both groups from one another. For instance, Chkhikvadze (1973) suggested that Paleocene *Hoplochelys* spp. from North America should be considered to be pan-chelydrids based on the presence of a cruciform plastron and the absence of a midline contact of the abdominal scutes, but Hutchison and Bramble (1981) later highlighted the affinities of *Hoplochelys* spp. with pan-kinosternoids, a conclusion supported by more recent analyses (e.g., Knauss et al. 2011). Similarly, the Late Cretaceous (Maastrichtian) *Emarginachelys cretacea* Whetstone, 1978 was originally described as a pan-chelydrid (Whetstone 1978b) but was later reinterpreted to be a pan-kinosternoid, although an explicit rationale was not provided for this assessment (e.g., Meylan and Gaffney 1989; Holroyd and Hutchison 2002; Holroyd et al. 2014). Although the available character evidence is conflicting, I here agree that *E. cretacea* is a pan-kinosternoid and therefore discuss it elsewhere (see Joyce and Bourque 2016). Finally, although *Tullochelys montana* Hutchison, 2013 from the early Paleocene of Montana was recently described as a new species of pan-chelydrid, I tentatively regard this as a pan-kinosternoid and therefore discuss it elsewhere as well (see Joyce and Bourque 2016).

For institutional abbreviations, see Appendix 1. Named pan-chelydrid genera are listed in Appendix 2.

Skeletal Morphology

Cranium

Chelydra serpentina is an extremely common turtle throughout North America, and skeletal material has been available to researchers for much of the past two centuries; however, early descriptions are lacking, beyond figures presented in Boulenger (1889). This situation was thoroughly mitigated by Gaffney (1972) who provided a systematic revision of the nomenclatural pertaining to the cranial anatomy of turtles and utilized *Chelydra serpentina* to illustrate most of the structures. The cranial anatomy of *Chelydra serpentina* and *Macrochelys temminckii* is otherwise discussed in Gaffney (1975b, 1979) as part of a general revision of the cranial anatomy of all turtles.

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Additional insights into the anatomy of *Macrochelys* spp. were finally provided by Thomas et al. (2014). Among fossil pan-chelydrids, the cranial anatomy is known for *Protochelydra zangerli* (Erickson 1973, 2010), *Chelydropsis murchisoni* (Pidoplichko and Tarashchuk 1960; Tarashchuk 1971; Broin 1977; Młynarski 1981b; Gaffney and Schleich 1994), *M. auffenbergi* (Dobie 1968), *M. schmidti* (Zangerl 1945; Whetstone 1978a) and *M. stricta* (Matthew 1924). Some additional skulls are known from the fossil record, but these are either preserved in slabs (e.g., Bell 1836; Meyer 1845) or represent poorly ossified juveniles (e.g., Meyer 1852, 1854, 1865; Paicheler et al. 1978) and therefore do not provide much anatomical information.

The skulls of pan-chelydrids are relatively large relative to the body and triangular when viewed dorsally. Extant *Macrochelys* are extremely macrocephalic and are therefore not able to fully withdraw their head inside the shell. The eyes of most taxa are oriented dorsolaterally (Figure 1B, C), but those of *Macrochelys* spp. are oriented laterally (Figure 1A). The upper temporal emargination ranges from intermediate to deep, but the lower temporal emargination generally remains shallow. Ridges and crenulations cover the skull surface in *Chelydra* spp.

The prefrontals are large and contact one another along the midline (Figure 1). The descending process is well developed and contacts the palatine and vomer distally and helps define a keyhole-shaped fissura ethmoidalis. The frontals are reduced in size and clearly do not contribute to the orbits in any taxon. The parietals are relatively large elements that form a broad descending process that contacts the palatines, pterygoids and epipterygoids ventrally and helps enclose the trigeminal foramen. The postorbitals are large elements that contribute to the rim of the orbit anteriorly, the upper temporal emargination posteriorly, and broadly contact the squamosals.

The premaxillae are small, paired elements that help define a pair of prepalatine foramina. The maxillae are large elements that often approach the quadratojugal closely posteriorly (Figure 1A) but never form an actual contact. The jugals are relatively elongate elements that symplesiomorphically contribute to the margin of the orbit (Figure 1A, B), with the notable exception of *Chelydropsis* spp. (Figure 1C). The quadrates are relatively large and frame the anterior margin of the cavum tympani. The squamosals universally lack an anterolateral contact with the parietals.

A premaxillary "hook" is particularly well developed among *Macrochelys* spp., relatively minor in *Chelydra serpentina* and absent in stem chelydrids. The premaxillae and maxillae, and sometimes the palatines, form intermediately broad and flat triturating surfaces, but some individuals of *Chelydropsis murchisoni* and *Protochelydra zangerli* exhibit extremely broad crushing surfaces. Pan-chelydrids consistently lack any signs of a secondary palate. The labial ridges are typically well developed, but minute lingual ridges are only present in some representatives of *Macrochelys*. The vomer is well developed and clearly separates the palatines. The pterygoids are large elements that broadly floor the otic region and posteriorly contact the basioccipital and exoccipitals. The external processes of the pterygoids are well developed and possess enlarged vertical flanges. The ventral exposure of the basisphenoid is relatively reduced, but never absent.

The cavum tympani of pan-chelydrids is formed by the quadrate, is relatively small and is often high oval in shape (Figure 1). The anterior margin of the vertically oriented antrum postoticum is formed by the quadrate. The incisura columella auris is enclosed but does not include the Eustachian duct. The trochlear process is mostly formed by the quadrate with a small contribution from the prootic. The process is clearly defined in all taxa but deeply protrudes into the temporal fossa in *Macrochelys* spp. The stapedial foramen is relatively large and placed relatively far to the anterior on top of the otic cavity. The supraoccipital forms an elongate and notable high crest that protrudes far beyond the level of the basioccipital.

The relatively small internal carotid artery enters the skull at the back of the skull in a foramen formed by the pterygoid. The exoccipitals form an enlarged bony flange that broadly covers the perilymphatic sack and that helps define the posterior jugular foramen. The remaining postotic fenestra, however, remains wide open. The exoccipitals and basioccipital otherwise help define two pairs of hypoglossal foramina.

The mandibles lack splenials and notable retroarticular processes. The triturating surface is generally simple but exhibits a well-formed midline "hook" in *Macrochelys* spp.

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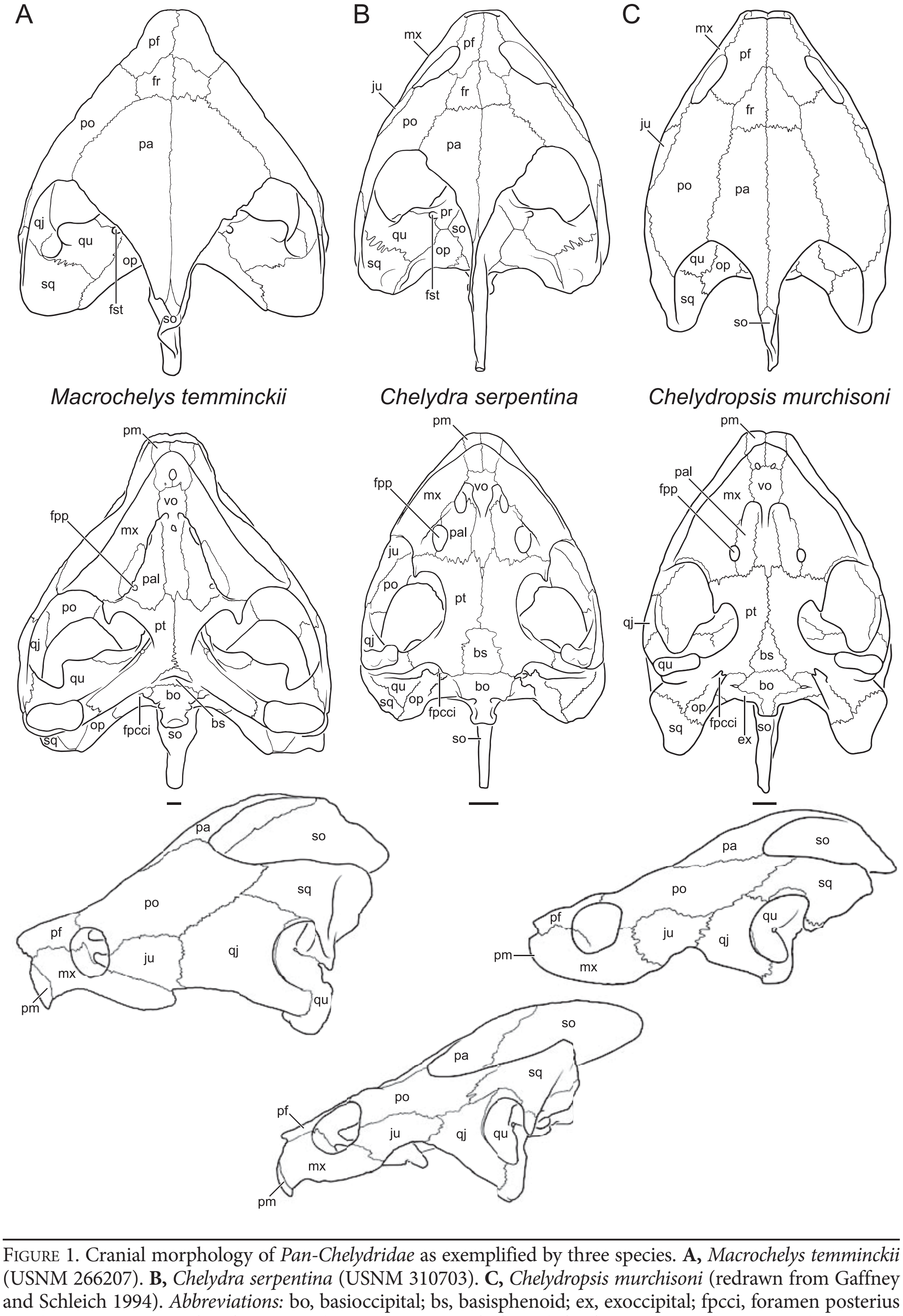

Macrochelys temminckii *Chelydra serpentina* *Chelydropsis murchisoni*

FIGURE 1. Cranial morphology of *Pan-Chelydridae* as exemplified by three species. **A,** *Macrochelys temminckii* (USNM 266207). **B,** *Chelydra serpentina* (USNM 310703). **C,** *Chelydropsis murchisoni* (redrawn from Gaffney and Schleich 1994). *Abbreviations:* bo, basioccipital; bs, basisphenoid; ex, exoccipital; fpcci, foramen posterius canalis carotici interni; fpp, foramen palatinum posterius; fr, frontal; fst, foramen stapedio-temporale; ju, jugal; mx, maxilla; op, opisthotic; pa, parietal; pal, palatine; pf, prefrontal; pm, premaxilla; po, postorbital; pr, prootic; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer. Scale bar approximates 1 cm.

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Shell

Original illustrations of extant shells are available for *Chelydra serpentina* (Meyer 1852; Boulenger 1889) and *Macrochelys temminckii* (Boulenger 1889), in addition to the ones provided herein. For fossil taxa, useful descriptions or illustrations of fossil shell material are provided for *Chelydropsis decheni* (Meyer 1852; Broin 1977), *Chelydropsis kusnetzovi* (Chkhikvadze 1987), *Chelydropsis murchisoni* (Bell 1836; Meyer 1845, 1852; Peters 1869; Winkler 1869; Młynarski 1980b; Gaffney and Schleich 1994), *Denverus middletoni* (Hutchison and Holroyd 2003) and *Protochelydra zangerli* (Erickson 1982). However, among fossil material, no taxon is sufficiently figured to allow presenting a rigorous reconstruction herein.

The carapaces of pan-chelydrids are generally broad and rounded, but well-developed nuchal and pygal notches are apparent in *Macrochelys temminckii*. The posterior margin is typically serrated. Traces of three carapacial keels are present in all species, with the exception of *M. temminckii*, which exhibits three rows of highly distinct tubercles that correspond with the scutes. Costal fontanelles are apparent in crown chelydrids, but absent in all stem representatives. The carapace normally consists of a nuchal, 8 neurals, 2 suprapygals, a pygal, 8 pairs of costals and 11 pairs of peripherals, but large amounts of variation are apparent in regard to the count of neural and suprapygal elements (Figure 2). The nuchal is typically a large, broad element and is characterized by the presence of riblike costiform processes that insert into peripheral III in crown chelydrids but are likely shorter in stem chelydrids. The neurals of most pan-chelydrids are broad and exhibit clear geometric shapes, but these elements are poorly defined and irregular in *Chelydra* spp. Suprapygal I is neural-like in its size and appearance, whereas suprapygal II is much broader and semilunate. The distal ends of the costal rib are broad and visible in ventral view below the peripherals. The bridge peripherals lack lateral keels and are therefore C-shaped in cross section. The bridge peripherals of stem chelydrids exhibit clear sockets for the peglike lateral processes of the plastron, but these are absent in crown representatives, as the bridge is fully ligamentous.

The carapace of pan-chelydrids is covered by a broad cervical, 5 hexagonal to rectangular vertebrals, 4 rectangular pleurals and 12 pairs of marginals (Figure 2). The pleural/marginal sulcus mostly coincides with the costal/peripheral suture and is therefore mostly invisible in extant taxa with costal fontanelles (Figure 2). The extant *Macrochelys temminckii* is known to possess up to three consecutive supramarginals that are situated between pleurals I–III and marginals IV–IX, but their sulci mostly coincide once again with the costal fontanelles, and presence of these scutes is therefore not documented in osteological specimens (Figure 1B). Supramarginals have also been reported for *Chelydropsis murchisoni*, but I cannot confirm this observation based on the available evidence.

The plastron of pan-chelydrids is notably cruciform and reduced in size relative to the carapace. In basal pan-chelydrids, the plastron is solid, but many midline fontanelles are apparent in extant species (Figure 2). The plastron consists of an entoplastron and a pair of epi-, hyo-, hypo- and xiphiplastra. The anterior and posterior plastral lobes are generally subtriangular, but the anterior lobe is notably broadened and rectangular in *Chelydropsis murchisoni*. The epiplastra are straplike and broadly cover the lateral sides of the hyoplastra. In basal pan-chelydrids, the entoplastron is a kite-shaped element that fully fills the space between the epiplastra and hyoplastra; however, in extant forms, this element is reduced to the shape of an anchor, thereby revealing a gaping entoplastral fontanelle. The bridge of basal pan-chelydrids is relatively narrow, and the plastron articulates with peripherals III–VII through pegs and sutures. In extant chelydrids, by contrast, the bridge is greatly reduced and the plastron articulates through ligaments with peripherals IV–VII in *Macrochelys temminckii* or peripherals V–VII in *Chelydra* spp. (Figure 2). The xiphiplastra mirror the epiplastra by being straplike but exhibit a deeply notched area at the contact with the hypoplastra.

Hutchison and Bramble (1981) presented an insightful analysis regarding the homology of scutes in pan-kinosternoid turtles, but they did not apply their newly developed nomenclature to pan-chelydrids, likely because they presumed these two clades to only be distantly related. If one applies the rationale of Hutchison and Bramble (1981) to pan-chelydrids, one must conclude that the scutes lacking a midline contact are the abdominals, as in pan-kinosternoids; that the

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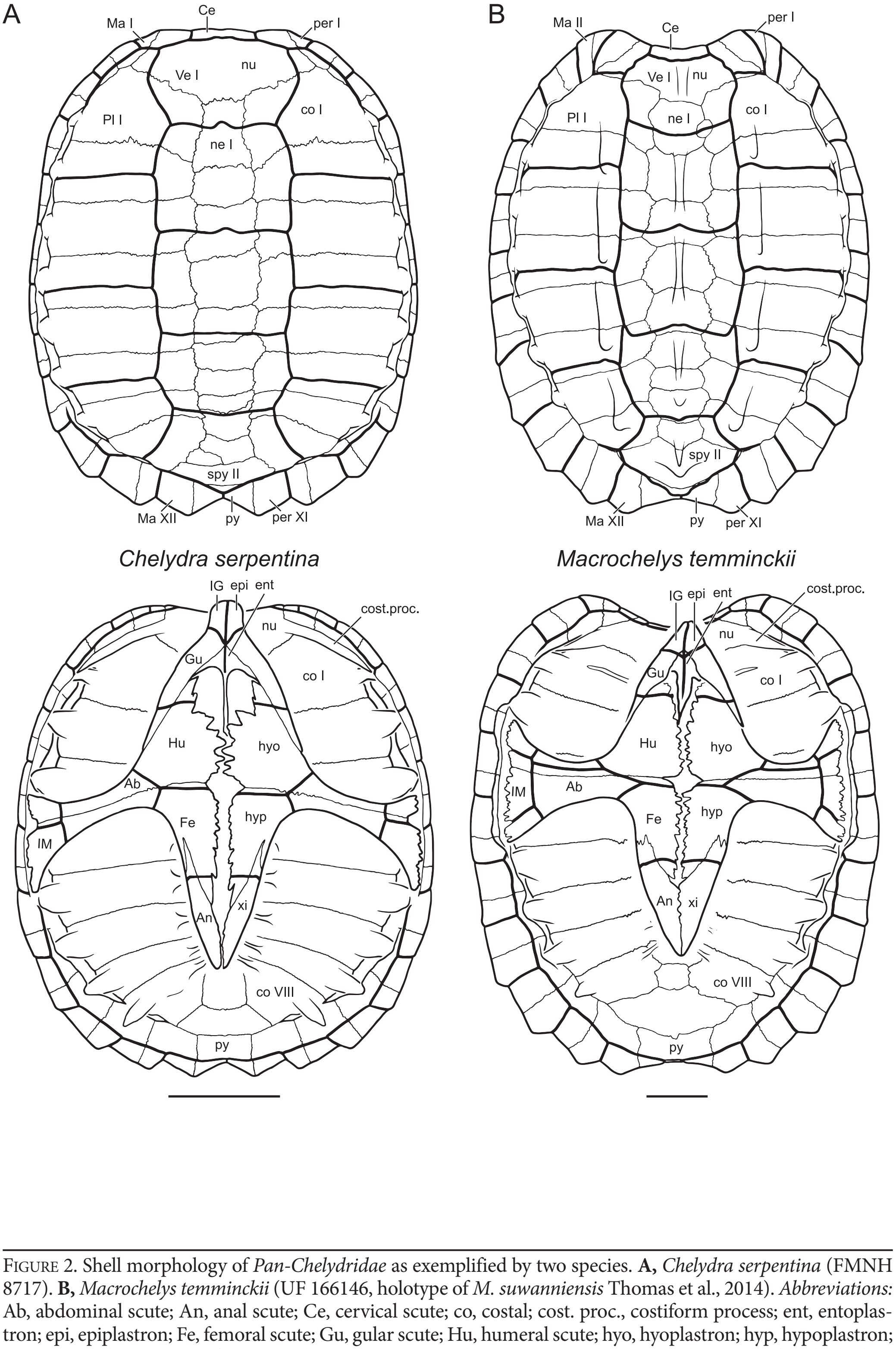

FIGURE 2. Shell morphology of *Pan-Chelydridae* as exemplified by two species. **A,** *Chelydra serpentina* (FMNH 8717). **B,** *Macrochelys temminckii* (UF 166146, holotype of *M. suwanniensis* Thomas et al., 2014). *Abbreviations:* Ab, abdominal scute; An, anal scute; Ce, cervical scute; co, costal; cost. proc., costiform process; ent, entoplastron; epi, epiplastron; Fe, femoral scute; Gu, gular scute; Hu, humeral scute; hyo, hyoplastron; hyp, hypoplastron; IG, intergular scute; IM, inframarginal scute; Ma, marginal scute; ne, neural; nu, nuchal; per, peripheral; Pl, pleural scute; py, pygal; spy, suprapygal; Ve, vertebrate scute; xi, xiphiplastron. Scale bar approximates 5 cm.

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scutes mostly associated with the hyoplastra are the humerals, as in most turtles; and that the scutes associated with the epiplastra are the gulars, as in most other turtles. This implies that the pectorals are lost, as in pan-kinosternoids. All available pan-chelydrids have two pairs of gulars anterior to the humerals. It is possible that these represent ancestral gulars and extragulars in an arrangement reminiscent of some baenid turtles (Joyce and Lyson 2015). However, given that the loss of extragulars seems to be a synapomorphy of Durocryptodira, I here interpret these two structures as gulars and neomorphic intergulars that emerged in concert with the "epiplastral beak," a tonguelike anterior protrusion formed by the epiplastra. Pan-chelydrids, therefore, have a pair of intergulars, gulars, humerals, abdominals, femorals and anals (Figure 2), but large amounts of variation are apparent, as already noted by Meyer (1852). The abdominals universally lack a midline contact but are split into two elements in *Macrochelys temminckii*. Three pairs of inframarginals typically cover the lateral aspects of the bridge, but only two pairs are found in *Chelydra* spp.

Postcranium

Williams (1950) described the cervical anatomy of extant chelydrids in detail, but I am unaware of any systematic descriptions to the remaining skeleton. *Chelydropsis decheni* and *Chelydropsis murchisoni* are known from many articulated skeletons from Oligocene of Rott, Germany (Meyer 1854, 1865; Lydekker 1889), and the Miocene of Öhningen (Meyer 1845, 1852; Winkler 1869), Steinheim (Młynarski 1980b) and Unterwohlbach (Gaffney and Schleich 1994), Germany, respectively, but the available descriptions of the postcranial skeleton are generally brief in the corresponding literature.

The cervical column consists of eight vertebrae, and the cervical formula is typically 1((2((3((4))5))6}}7))8). As in most durocryptodirans, the cervicals are low and broad, ribs are lacking, transverse process are places at the anterior end of the centrum, the posterior cervicals are well-developed ventral processes and cervical VIII possesses elongate and recurved postzygapophyses. The tail is notably elongate and adorned by well-developed chevrons. The anterior, procoelous caudals are separated from the posterior, opisthocoelous caudals by a single amphicoelous caudal, typically the third (Gaffney 1985). The coracoids are slightly expanded distally, and the glenoid lacks a distinct neck. The ilium is tilted slightly to the posterior, is straight and may show a minor hint of a thelial process midshaft. The lateral pubic and ischial processes are well developed. The thyroid fenestra is typically subdivided by the pubes, ischia and calcified cartilages. The epipubis is similarly present but typically consists of calcified cartilage. The hands and feet generally resemble those of most other durocryptodirans by being intermediate in length, having a phalangeal formula of 2-3-3-3-3 and having five claws in the hand but only four in the foot.

Phylogenetic Relationships

Thomas et al. (2014) recently highlighted that molecular data allow recognizing three populations of extant *Macrochelys*, with the population from the Suwannee River of Florida, USA, being sister to the remaining two populations from the Apalachicola and greater Mississippi drainage basins farther to the west. Whether these three populations should be regarded as three (Thomas et al. 2014), two (Folt and Guyer 2015) or one species (Turtle Taxonomy Working Group 2014) is currently under debate. I am unaware of a molecular study that investigates the three species of *Chelydra*, but it is reasonable to presume that the two taxa from Central and South America are each other's closest relatives.

The phylogenetic relationships of fossil pan-chelydrids remains poorly resolved. Gaffney (1975b) presented a phylogenetic analysis of five "pan-chelydrids," but this analysis is highly suboptimal using modern standards because the pan-chelydrid *Protochelydra zangerli* was presumed to be the outgroup, *Platysternon megacephalum* was presumed to be within the ingroup and an explicit matrix is lacking. The results of this analysis imply that the European *Chelydropsis murchisoni* (*Macrocephalochelys pontica* of Gaffney 1975b) is closer to *Macroclemys temminckii* than *Chelydra serpentina*, and therefore also a crown chelydrid.

Whetstone (1978a) provided a small analysis of the three species of *Macrochelys* he was aware of using cladistic arguments and hypothesized that *M. auffenbergi* and *M. schmidti* are the successive

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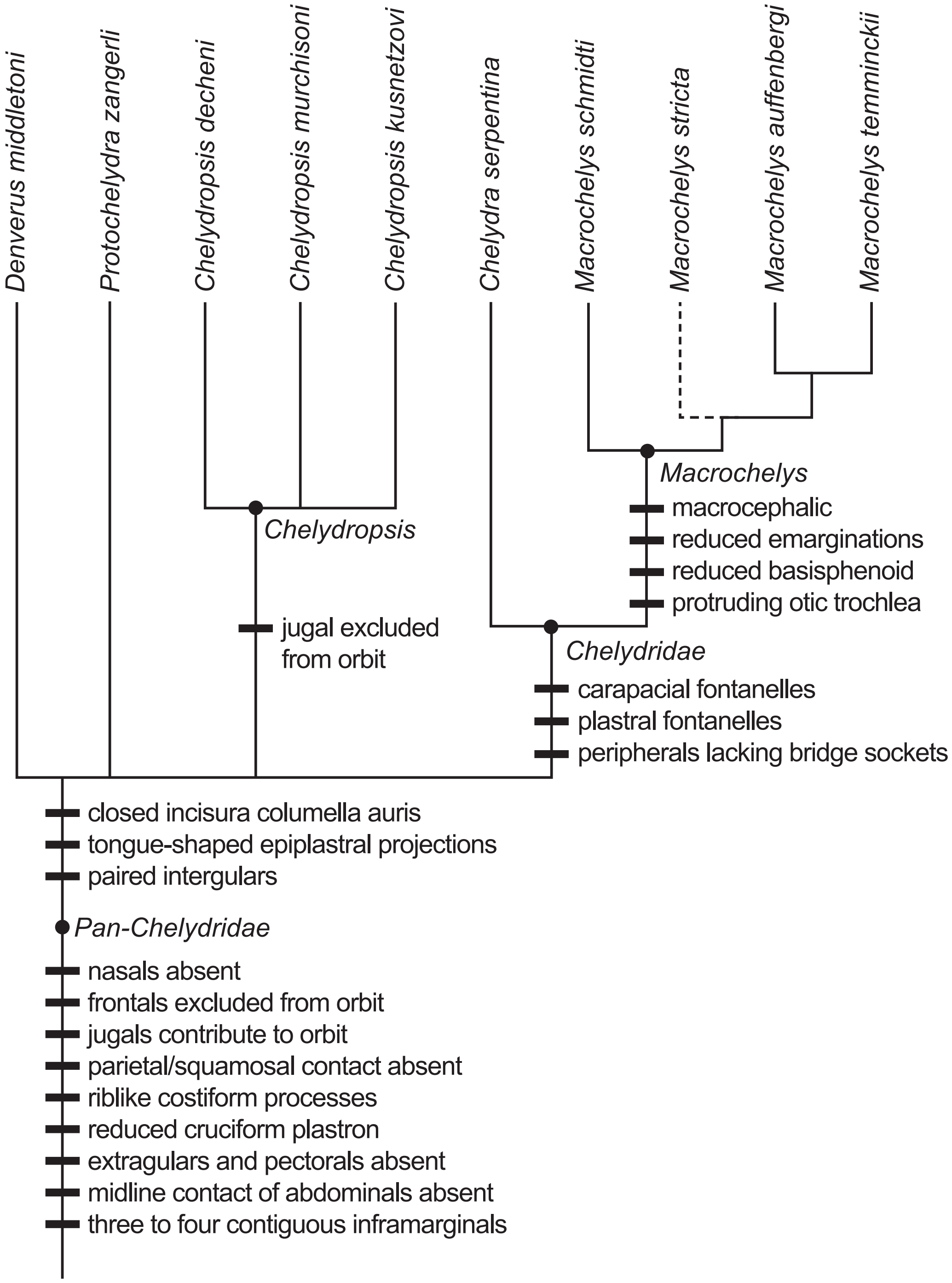

FIGURE 3. A phylogenetic hypothesis of valid pan-chelydrid taxa with select diagnostic characters for the most important clades. Given that a global phylogenetic analysis is still outstanding for the group, dashed lines highlight the ad hoc placement of fossils within the chelydrid crown group. The topology within *Macrochelys* follows the manual analysis of Whetstone (1978a).

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outgroups of *M. temminckii*. This topology incidentally corresponds with the appearance of these taxa in the fossil record, but this analysis too lacks rigorous testing.

Hutchison (2008) more recently presented a character/taxon matrix and a phylogenetic hypothesis for a selection of pan-chelydrid taxa but did not provide any of the parameters normally associated with parsimony analysis, such as the selection of an outgroup or use of ordered characters. As part of this study, I subjected the matrix to parsimony analysis but was not able to retrieve a tree with any resolution. Given a complete lack of alternative phylogenetic analyses, I utilize the highly reasonably topologies presented by Whetstone (1978a) for *Macrochelys* combined with Hutchison (2008) for *Pan-Chelydridae* (Figures 3 and 4) but await a more rigorous phylogenetic assessment in the future.

Paleoecology

All extant chelydrids are classified as aquatic bottom walkers (Zug 1971). *Chelydra* spp. inhabit all types of freshwater aquatic habitats, especially those with low energy, but will readily venture onto land in search of new habitat. *Macrochelys temminckii*, by contrast, prefers rivers with deeper water, and only females return to land to lay their eggs (Ernst and Barbour 1989). These two observations may explain the wide distribution of *Chelydra* from southeastern Canada to northern Colombia and the proclivity of *Macrochelys* to split into lineages that correspond to river drainage systems (Thomas et al. 2014). Fossil pan-chelydrids from the Late Cretaceous and Paleocene of North America are typically found in ponded environments (pers. obs.) and therefore seem to have been more ecological similar to extant *Chelydra* spp. by preferring bodies of water with low energy.

Whereas *Chelydra* spp. are true omnivores that actively seek prey, *Macrochelys temminckii* is a highly carnivorous ambush predator that lures prey into its mouth with its worm-shaped tongue (Ernst and Barbour 1989). The skulls of various fossil *Macrochelys* spp. with time increasingly resemble those of extant *M. temminckii* by being macrocephalic, having a notably midline “hook” and lacking broad triturating surfaces; it is therefore reasonable to infer similar dietary preferences. The broad and flat triturating surfaces found in some individuals of *Protochelydra zangerli* (Erickson 2010) and *Chelydropsis murchisoni* (undescribed material housed at MNHN), by contrast, reveal that these basal pan-chelydrids were specialized molluscivores, similar to various baenids (Joyce and Lyson 2015), testudinoids (Joyce and Bell 2004) or bothremydids (Gaffney et al. 2006).

Paleobiogeography

The early record of pan-chelydrids is restricted to North America. Remains have been reported from as early as the Turonian to Utah, USA (Hutchison 1998), but these have not yet been figured or described; therefore, I cannot replicate this record. The oldest documented pan-chelydrids are cataloged fragments from the Santonian of Alberta, Canada (Brinkman 2003; Figure 5). Figured or cataloged fragments are otherwise known from the Campanian of Alberta (Brinkman 2003; Brinkman and Eberth 2006), Utah (Hutchison et al. 2013) and Coahuila, Mexico (Rodriguez-de la Rosa and Cevallos-Ferriz 1998), and from the Maastrichtian of Alberta (Brinkman 2003; Brinkman and Eberth 2006), Montana (Holroyd and Hutchison 2002; Holroyd et al. 2014), North Dakota (Holroyd and Hutchison 2002) and Wyoming (Holroyd and Hutchison 2002), USA. Other fragmentary remains reported from the Campanian of Coahuila (Brinkman and Rodriguez de la Rosa 2006) likely represent pan-kinosternoid remains instead (D.B. Brinkman, pers. comm., 2015). I agree with all previous authors that the Late Cretaceous material is undiagnostic at the species level and therefore refer it to *Pan-Chelydridae* (Figure 5).

Following the Cretaceous/Tertiary extinction event, the fossil record of pan-chelydrids improves dramatically throughout North America, though for unclear reasons (Figure 5). In addition to providing more undiagnostic material (Holroyd and Hutchison 2002; Holroyd et al. 2014), Early Paleocene (Puercan North American Land Mammal Age [NALMA], Danian) sediments in Colorado, USA, yielded skeletal remains of the small-bodied pan-chelydrid *Denverus middletoni* Hutchison and Holroyd, 2003. The significantly larger pan-chelydrid *Protochelydra zangerli* was originally reported from the Late Paleocene (Tiffanian

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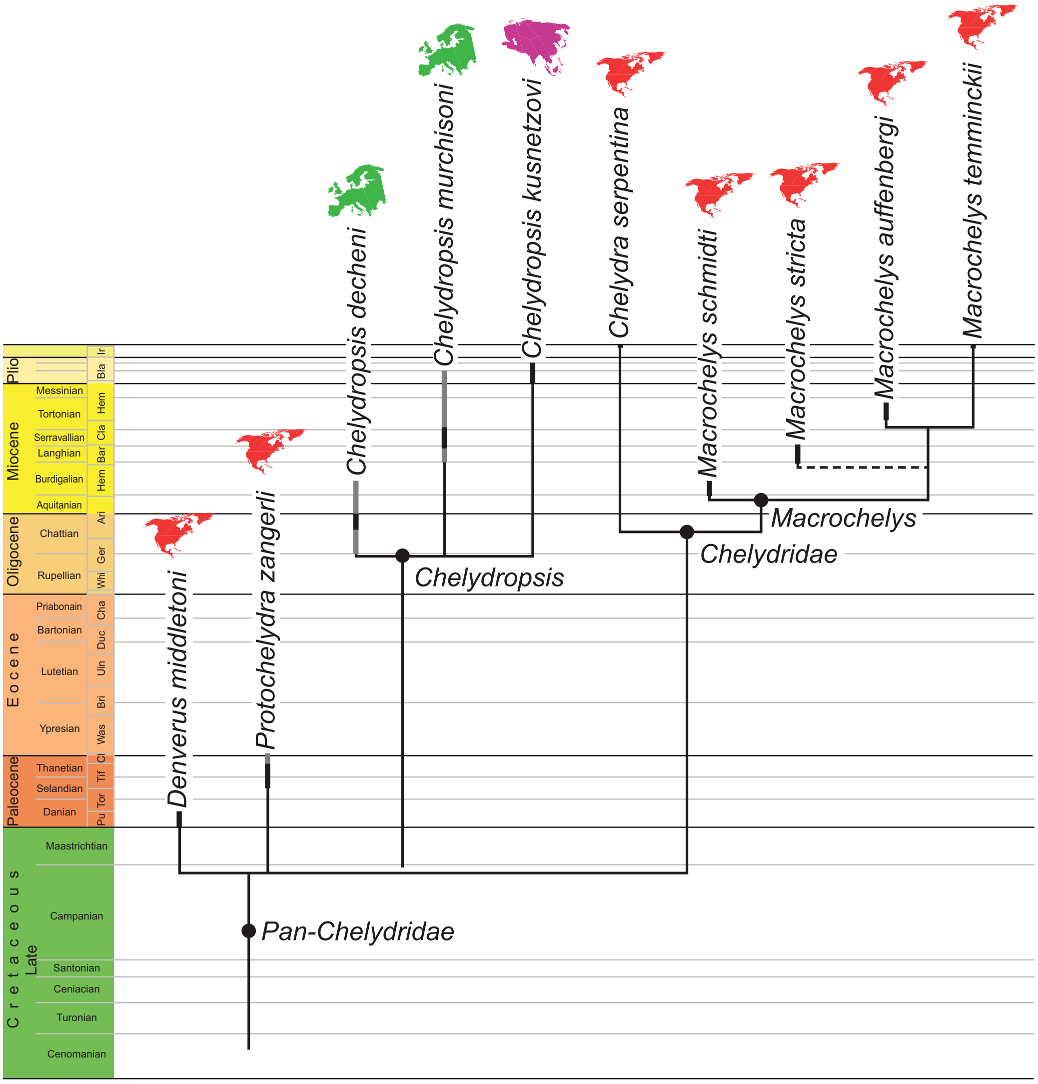

FIGURE 4. The stratigraphic and biogeographic distribution of valid pan-chelydrid taxa. Black lines indicate temporal distribution based on type material. Gray lines indicate temporal distribution based on referred material. The topology is a combination of those proposed by Whetstone (1978a) and Hutchison (2008).

NALMA, Selandian–Thanetian) of North Dakota (Erickson 1973, 1982, 1984, 2010) but has since been recovered from the Late Paleocene of Alaska, USA (Hutchison and Pasch 2004), and Alberta (Brinkman 2013). Bartels (1983) reported two complete shells of *P. zangerli* from the Late Paleocene of Wyoming, but figures are missing; therefore, I refer this material to *Pan-Chelydridae*. I furthermore agree that the holotype of *Hoplochelys caelata* Hay, 1908a is a chelydrid (e.g., Hutchison 2008) but find this taxon to be undiagnostic (see Systematic Paleontology) and refer it to *Pan-Chelydridae* as well. The Eocene record of *Pan-Chelydridae* only consists of a few fragments from Wyoming (Holroyd et al. 2001) and Oregon, USA (Hanson 1996; Figure 5). Hutchison (2008) informally noted the presence of fragments from the Eocene of Ellesmere Island, Canada, but no specimens are referred. Eaton et al. (1999) similarly reported fragments from Utah, but these lack vouchers; therefore, I cannot replicate this claim. Hutchison (1992) finally reports chelydrids from

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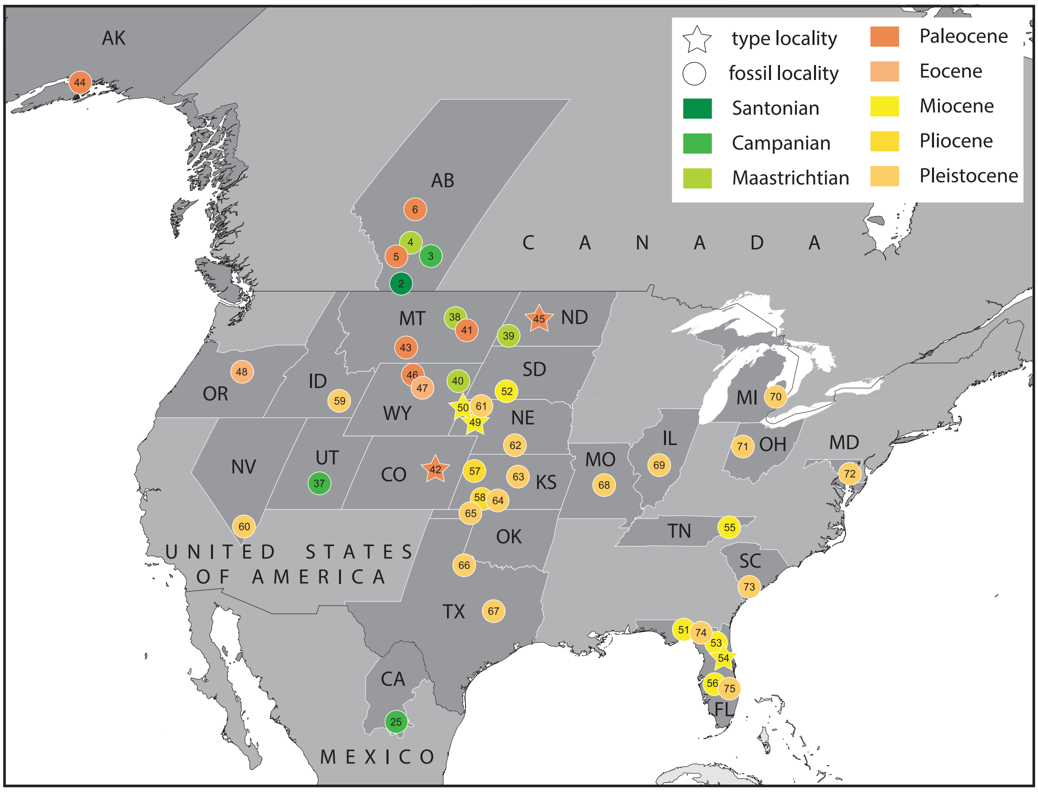

FIGURE 5. The geographic distribution of figured pan-chelydrids from North America. Stars mark the type localities of valid taxa. Locality numbers are cross-listed in Appendix 3. *Abbreviations:* AB, Alberta; AK, Alaska; CA, Coahuila; CO, Colorado; FL, Florida; ID, Idaho; IL, Illinois; KS, Kansas; MI, Michigan; MD, Maryland; MO, Missouri; MT, Montana; ND, North Dakota; NE, Nebraska; NV, Nevada; OH, Ohio; OK, Oklahoma; OR, Oregon; SC, South Carolina; SD, South Dakota; TN, Tennessee; TX, Texas; UT, Utah; WY, Wyoming.

the Oligocene of North America (Figure 5), but I once again cannot reproduce these claims, as no material is figured or listed. I agree with Hutchison (2008) that *Acherontemys heckmani* Hay, 1899 is not a pan-chelydrid (e.g., Hay 1908b), but rather a testudinoid.

The Neogene record of North American pan-chelydrids consists mostly of fragments, but some localities provide well-preserved skull remains, which document the emergence of the *Macrochelys* lineage. These include *Macrochelys schmidti* Zangerl, 1945 from the Early Miocene of Nebraska, USA (Zangerl 1945; Whetstone 1978a); *Macrochelys stricta* Matthew, 1924 from the Middle Miocene of Nebraska (Matthew 1924); and *Macrochelys auffenbergi* Dobie, 1968 from Late Miocene of Florida, USA, which includes extensive postcranial remains (Figure 5). Undetermined fragments referable to *Macrochelys* indet. are otherwise known from the Middle Miocene of Florida (Thomas et al. 2014); the Late Miocene of South Dakota, USA (*Macrochelys temminckii* of Zangerl 1945), and Florida (Thomas et al. 2014); the Pliocene of Kansas (*Macroclemys temminckii* of Hibbard 1963); and the Pleistocene of Texas, USA (*Macrochelys temminckii* of Hay 1911), and Florida (Auffenberg 1957; Thomas et al. 2014). Parmley (1992) reported fragmentary remains from the Late Miocene of Nebraska but did not provide figures to support this claim. Up to three species of *Macrochelys* that possibly diverged from one another in the Late Miocene currently inhabit large rivers across the southeastern United States (Thomas et al. 2014), but given current debates regarding the validity of all three taxa (e.g., Folt and Guyer 2015), I here recognize a single species, *Macrochelys temminckii* (Troost in Harlan 1835).

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The remaining Neogene pan-chelydrid record consists of rarely figured postcranial remains that have been referred to the *Chelydra serpentina* lineage (Figure 5). Given the broad distribution of *Chelydra serpentina* in North America today (Ernst 2008), it is plausible that these fragments indeed document a single lineage leading up to the extant species, but the available material is insufficient at present to allow reconstructing the sequential evolution of modern traits. Given that the early postcranial morphology of the *Macrochelys* lineage remains obscure, I herein refer all fragments from the Miocene to *Chelydridae* indet. These records include fossils from the Middle Miocene of Nebraska (Holman and Sullivan 1981) and from the Late Miocene of Florida (Bourque 2013; Thomas et al. 2014) and Tennessee, USA (Bentley et al. 2011). Given that the *Macrochelys* lineage is well established throughout the Miocene, I presume that fossils representing the *Chelydra* and *Macrochelys* lineage are more easily distinguishable by the Pliocene. I therefore refer all fragmentary material from the Plio/Pleistocene to *Chelydra* indet. This includes fragments from the Pliocene of Kansas (Hibbard 1934, 1939, 1963; Galbreath 1948) and from the Pleistocene of Idaho (Pinsof 1998), Nevada (Van Devender and Tessmann 1975), Nebraska (Preston 1979), Kansas (Galbreath 1948; Hibbard and Taylor 1960; Schultz 1965; Preston 1971, 1979; Holman 1972), Oklahoma (Preston 1979), Texas (Holman 1964), Missouri (Parmalee and Oesch 1972), Illinois (Holman 1966), Michigan (Wilson 1967), Ohio (Holman 1986), Maryland (Cope 1870; Hay 1908b) and South Carolina (Dobie and Jackson 1979). The only exceptions are rich skeletal remains of a large-bodied fossil chelydrid from the Pleistocene of Florida (*Macrochelys floridana* of Hay 1907; *Chelydra floridana* of Thomas et al. 2014), which I believe to broadly overlap in size and morphology with the extant Florida snapping turtles (pers. obs. of material at UF) and therefore refer to *Chelydra serpentina*. I herein do not list Holocene remains (see Ernst 2008 for a summary). Up to three species of *Chelydra* currently inhabit a broad land area from southeastern Canada to Colombia (Ernst 2008), but the dispersal event from North America to South America that occurred as part of the Great American Interchange has not yet been documented with fossils.

The early record of pan-chelydrids in Europe is somewhat obscured by the fragmentary nature of the available record and changing taxonomic assessments. Groessens-Van Dyck (1984) figured fragmentary remains from the Paleocene of Belgium, but I cannot confirm their pan-chelydrid identity, whereas others seem to have ignored these reports (e.g., Lapparent de Broin 2001; Danilov 2005). Additional fragments from the Paleocene of Belgium (Groessens-Van Dyck and Schleich 1988) are not figured, and their pan-chelydrid affinities cannot be confirmed either. Lapparent de Broin (2001) interprets various remains from the Cretaceous to Eocene of Europe as being "chelydroid" in nature, but given the vague definition of the term chelydroid, it is unclear to which clade she is referring. Lapparent de Broin (2001) nevertheless notes that these fragments lack derived "chelydrid" traits, and it is therefore safe to presume that these do not represent the clade *Pan-Chelydridae*, but perhaps another clade, such as Macrobaenidae (Danilov 2008). Lapparent de Broin (2001) mentions the presence of *Pan-Chelydridae* in the Late Eocene of France, but this record remains to be described or figured. Reinach (1900) finally reported a single pan-chelydrid costal fragment from the Early Oligocene of Germany, but this originates from marine sediments, and I see similarities with cheloniid sea turtles (contra Broin 1977) as the fragment in question is notably thick, displays a highly spongy internal structure and reveals the former presence of a strong rib head. It therefore seems all but certain that pan-chelydrids were not present in Europe until the Early Oligocene.

Some pan-chelydrid specimens have been reported from the Late Oligocene of France and Germany (Figure 6). Given that there is only evidence for a single lineage of pan-chelydrid in Europe, I here refer all undiagnostic material from France (see Broin 1977 for an extensive summary of French localities) and Germany (Karl et al. 2011) to *Chelydropsis* and otherwise only recognize one early taxon, *Chelydropsis decheni*, from France (Broin 1977) and Germany (Meyer 1852, 1854, 1865). Additional fragments have been reported from throughout Germany (Schleich 1988; Schleich and Groessens van Dyck 1988; Karl 1990), but I cannot confirm their specific identity with the available evidence.

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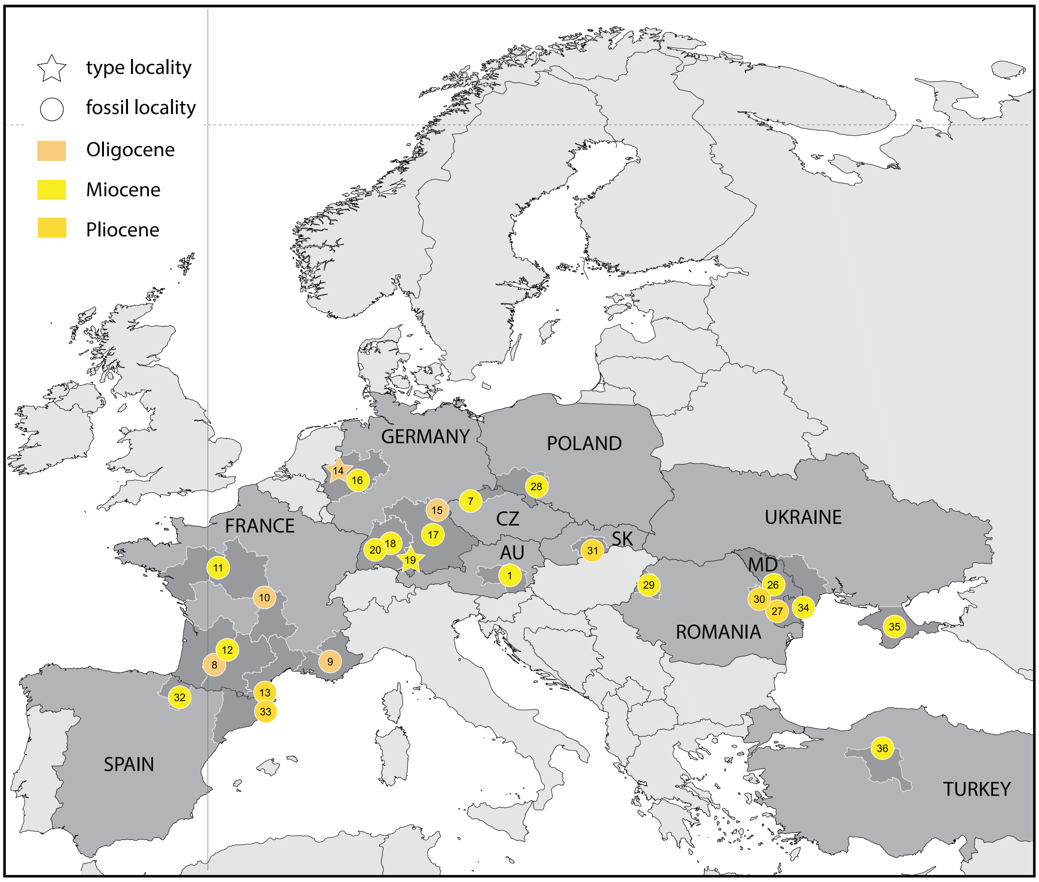

FIGURE 6. The geographic distribution of figured pan-chelydrids from Europe. Stars mark the type localities of valid taxa. Locality numbers are cross-listed in Appendix 3. *Abbreviations:* AU, Austria; CZ, Czech Republic; MD, Moldova; SK, Slovakia.

Miocene sediments across much of Europe have yielded beautifully preserved pan-chelydrid material, including many complete skeletons and crania (e.g., Bell 1836; Meyer 1845; Winkler 1869; Broin 1977; Młynarski 1980b; Gaffney and Schleich 1994; Figure 6). As for all Miocene material, I assign all undiagnostic material to *Chelydropsis* sp., including remains from Austria (Böhme and Vasilyan 2014), the Czech Republic (Laube 1900, 1910; Schlosser and Hibsch 1902), France (see Broin 1977 for a detailed list of localities), Germany (Groessens-Van Dyck and Schleich 1985; Schleich 1986; Strauch 1990; Karl 2013), Moldova (Khosatzky and Redkozubov 1989), Romania (Młynarski 1966), Ukraine (Khosatzky 1949, 1966, 1982; Chkhikvadze 1980) and, though not technically part of Europe, nearby Anatolia, Turkey (Paicheler et al. 1978). I here refer diagnostic early Miocene remains from Spain to *Chelydropsis decheni* (Murelaga et al. 1999; Murelaga et al. 2002) and Middle to Late Miocene remains from Austria (Peters 1855, 1868, 1869; Gross 2002), France (Broin 1977; Lapparent de Broin 2000), Germany (Bell 1836; Meyer 1845, 1852; Winkler 1869; Fraas 1870; Fuchs 1939; Młynarski 1980b; Schleich 1981; Gaffney and Schleich 1994; Klein and Mörs 2003), Poland (Młynarski 1981a, 1981b) and Ukraine (Pidoplichko and Tarashchuk 1960; Tarashchuk 1971) to *Chelydropsis murchisoni*. Due to a lack of figures, I am unable to confirm the specific identity of additional fragmentary material from Austria (Teppner 1914, 1915), Germany (Schleich 1981, 1982, 1985) and Moldova (Khosatzky and Tofan 1970). As political boundaries have changed throughout the 20th century, it is worth noting that no pan-chelydrids have been reported from modern-day Hungary (contra Szalai 1934).

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FIGURE 7. The geographic distribution of figured pan-chelydrids from central Asia. Stars mark the type localities of valid taxa. Locality numbers are cross-listed in Appendix 3. *Abbreviations*: EK, East Kazakhstan; NK, North Kazakhstan; PA, Pavlodar.

Although the Pliocene record is far less extensive, pan-chelydrids are present throughout Europe during this time period. I once again refer undiagnostic fossils to *Chelydropsis* indet., including material from France (Aymar 1992), Moldova (Khosatzky and Redkozubov 1986, 1989), Romania (Macarovici and Vancea 1959; Młynarski 1969), Slovakia (Młynarski 1963; Danilov et al. 2012) and Spain (Claude et al. 2014; Figure 6). The Ukrainian material mentioned previously is poorly dated but may be Pliocene as well. Pending better documentation, I disregard fragmentary material reported from Georgia (Syromyatnikova et al. 2013), Germany (Mörs 2002), Moldova (Khosatzky 1966), Slovakia (Młynarski 1963), Ukraine (Khosatzky 1966, 1982) and Russia (Syromyatnikova et al. 2013). Pan-chelydrids completely vanish from Europe by the Pleistocene, likely due to climatic cooling.

The Asiatic pan-chelydrid record is still poorly documented (Figure 7). Nessov (1987) reported the possible presence of pan-chelydrids from the Coniacian of Uzbekistan, but this claim was never further substantiated (Sukhanov 2000). Over the course of the past decades, many pan-chelydrid fragments have been reported from the Early Oligocene (Chkhikvadze 1971, 1973), Late Miocene (Chkhikvadze 1971, 1973) and Pliocene (Khosatzky 1944, 1967, 1982; Gaiduchenko and Chkhikvadze 1985; Chkhikvadze 1987) of northeastern Kazakhstan. However, only a few fragments have been described or figured to date, and I am therefore only able to recognize one out of three named taxa, *Chelydropsis kusnetzovi*. I refer all other material once again to *Chelydropsis* indet.

Given that the early record of pan-chelydrids and pan-kinosternoids took place in North America, it seems all but certain that pan-chelydrids originated in situ in North America and secondarily dispersed to Europe and Asia. This conclusion contrasts earlier considerations of Chkhikvadze (1973), who derived pan-chelydrids in Asia from groups such as the Sinemydidae.

Hutchison (1998) hypothesized that pan-chelydrids originated in North America and migrated from North America to Europe in the Paleocene only to go extinct by the Eocene; however, as noted previously, the Paleocene pan-chelydrid record from Europe is dubious at best, and this hypothesis therefore lacks any basis. Instead, it seems that pan-chelydrids entered Eurasia only once (Hutchison 2000) at some point prior to the Late Oligocene. Given that the oldest records from Asia and Europe are nearly contemporary, it is not possible to distinguish the direction of migration.

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Systematic Paleontology

Valid Taxa

See Appendix 4 for the hierarchical taxonomy of *Pan-Chelydridae* as described in this work.

Pan-Chelydridae Joyce et al., 2004

Phylogenetic definition. Following Joyce et al. (2004), the term *Pan-Chelydridae* is herein referred to the total clade of *Chelydridae* (see *Chelydridae* below).

Diagnosis. Representatives of *Pan-Chelydridae* are currently diagnosed relative to other turtles by the symplesiomorphic absence of nasals, exclusion of the frontals from the orbit, inclusion of the jugals in the orbit, lack of a parietal/squamosal contact, presence of elongate costiform processes, a reduced, cruciform plastron, absence of extragulars and pectorals, lack of a midline contact of the abdominals, presence of three to four contiguous inframarginals, and the derived presence of an enclosed incisura columella auris, tongue-shaped epiplastral projections and paired intergulars (Figure 3).

Chelydropsis Peters, 1868

Type species. *Chelydropsis carinata* Peters, 1868.

Diagnosis. *Chelydropsis* can be diagnosed as pan-chelydrid by the full list of characters given above for that taxon. *Chelydropsis* is currently differentiated primarily from other pan-chelydrids by the exclusion of the jugal from the orbit.

Comments. A series of well-preserved skeletons from the Germany localities of Öhningen and Rott were highly instrumental in the early phases of fossil turtle research, and they clearly revealed their pan-chelydrid affinities and faunal links between North America and Europe (Bell 1836; Meyer 1845, 1852). Although two species of extant chelydrids were known at the time, most early researchers do not seem to have been familiar with the newly described *Macrochelys temminckii*. They therefore only made comparisons with the abundantly known *Chelydra serpentina* (Linnaeus, 1758) and referred their new fossils to *Chelydra*. Peters (1868) noted systematic differences between new, beautifully preserved specimens from Austria and all previously described material and felt justified in naming of a new genus for his new species, *Chelydropsis*. His list of diagnostic characters includes the presence of a horizontally split nuchal, a double row of marginals, and well-defined neurals. I here agree with Williams (1952) and Młynarski (1976) that the split nuchal of this taxon seems to be a taphonomic artifact, and I cannot find any clear evidence for the presence of supramarginals, here or elsewhere and despite claims to the contrary (e.g., Broin 1977; Hutchison 2008). Most diagnostic characters of Peters (1868) therefore lack a factual basis.

Zangerl (1945) noted that all known European pan-chelydrids seems to be distinct from the two extant North American taxa, but not until Chkhikvadze (1971) did it become common practice to unite all European material within *Chelydropsis*. Broin (1977) argued for the presence of two European species groups within *Chelydropsis*: the Oligo/Miocene *decheni-sanctihenrici* group and the Mio/Pliocene *murchisoni* group. Using the same characters, Chkhikvadze (1999) further emphasized the distinctness of these two groups by creating the taxon *Chelydrasia* for the *decheni-sanctihenrici* group, with the Asian *Chelydropsis minax* serving as the type species. Although some argued that *Chelydrasia* should be restricted to Asiatic forms to render a European *Chelydropsis* (e.g., Murelaga et al. 2002), others have followed the classification of Chkhikvadze (e.g., Hutchison 2008).

Although a rigorous phylogenetic analysis is still outstanding, I here only recognize a single lineage throughout the fossil record of Europe. Furthermore, the "*decheni-sanctihenrici* group" seems to be ancestral relative to the "*murchisoni* group." Although I agree that the development of Asiatic pan-chelydrids likely took place somewhat separately from those in Europe, it is most parsimonious to assume that they are related with European forms, although the available fossil evidence is far too fragmentary to allow testing this hypothesis at the moment. To avoid rendering *Chelydropsis* paraphyletic, I unite all Eurasian material into a single taxon, *Chelydropsis*.

Chelydropsis decheni (Meyer, 1852) (= *Chelydropsis sanctihenrici* Broin, 1977 = *Chelydropsis apellanizi* Murelaga et al., 1999)

Taxonomic history. *Chelydra decheni* Meyer, 1852 (new species); *Chelydra dacheni* Młynarski, 1969 (incorrect spelling of species epithet); *Chelydropsis decheni* Broin, 1977 (new combination); *Chelydrasia decheni* Hutchison, 2008 (new combination).

Type material. IPB Ro4016 (holotype), a relatively complete skeleton on two slabs lacking the anterior tip of the skull, parts of the peripheral series and the posterior tip of the tail (Meyer 1852, pls. 18 and 19; Böhme and Lang 1991, fig. 1).

Type locality. Rott, North Rhine-Westphalia, Germany (Figure 6); Paleogene European Mammal Zone (MP) 30, Chattian, Late Oligocene (Aguilar et al. 1997).

Referred material and range. Late Oligocene (Chattian) of Rott (type locality), Germany (Meyer 1854, 1865; Lydekker 1889); Late Oligocene (Chattian) of the Department of Bouches-du-Rhône, France (type material of *Chelydropsis sanctihenrici*; Broin 1977); Early Miocene (Burdigalian) of Navarre, Spain (type material of *Chelydropsis apellanizi*; Murelaga et al. 1999; Murelaga et al. 2002).

Diagnosis. *Chelydropsis decheni* can be diagnosed as a representative of *Chelydropsis* by the isolation of the jugal from the orbit. *Chelydropsis decheni* is currently differentiated from *Chelydropsis murchisoni* by the presence of broader peripherals, a less serrated posterior carapacial margin, an anteroposteriorly wider bridge and a triangular anterior plastral lobe. *Chelydropsis decheni* is primarily distinguished from *Chelydropsis kusnetzovi* using temporal and biogeographic considerations (see Comments below).

Comments. *Chelydropsis decheni* is based on a relatively well-preserved skeleton from the Late Oligocene of Rott, Germany

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(Meyer 1852). Although Meyer (1854, 1865) soon after described two additional skeletons from the type locality, no further material has been recovered ever since (Böhme and Lang 1991). *Chelydropsis decheni* can most readily be distinguished from the younger *Chelydropsis murchisoni* by its overall smaller size and the symplesiomorphic presence of a cruciform plastron with pointed anterior and posterior lobes, as opposed to the greatly broadened anterior plastral lobe of *Chelydropsis murchisoni*. The three available specimens from Rott are notable, as they represent differently sized juveniles with different ontogenetic stages (Meyer 1854, 1865).

More than 100 years after the description of *Chelydropsis decheni*, Broin (1977) documented new material from the Late Oligocene locality of Saint-Henri near Marseille in southern France. Broin (1977) highlighted many similarities between *Chelydropsis decheni* and the new French material but nevertheless decided to create a new taxon, *Chelydropsis sanctihenrici*, because the French material was larger, had a wider bridge, lacked fontanelles, had a less developed pygal notch and exhibited stronger carapacial ornamentation. However, Broin (1977) already noted that most of these characters could be related to ontogeny.

More recently, Murelaga et al. (1999, 2002) described new material from the Early Miocene (Burdigalian) of Navarre in northern Spain. Although the available material is highly fragmentary, it is apparent that this taxon exhibits the narrow cruciform plastron typical of *Chelydropsis decheni* and *Chelydropsis sanctihenrici*. Murelaga et al. (1999) furthermore diagnosed a new taxon, *Chelydropsis apellanizi*, based on nuanced differences in the thickness of the shell, the extent of the pygal notch and the relative length of the pectoral/abdominal sulcus compared with the femoral/abdominal sulcus. However, the fragmentary material available barely supports these observations.

Although the taxonomy of extant chelydrids is still far from resolved, it is apparent that chelydrids are not a speciose group. Among extant faunas, three species of *Chelydra* are currently recognized to occur in three distinct geographic areas throughout the Americas (Turtle Taxonomy Working Group 2014). Three distinct species of *Macrochelys* have similarly been recognized, but these, once again, occur in three nonoverlapping biogeographic areas (Thomas et al. 2014). Extant chelydrids therefore seem to diverge into separate lineages in response to allopatry, but the lack of extant species richness reveals that lineages typically converge when minor geographic barriers collapse. The only exception, apparently, is the permanent split between the *Chelydra* and *Macrochelys* lineages.

For much of the Tertiary, mainland Europe was fragmented by mountain ranges and epicontinental seas, but most of these barriers did not divide the continent completely and did not persists for much time. Although it is possible that European pan-chelydrids speciated in response to these geographic barriers, I find it intriguing that not a single European locality has yielded two sympatric pan-chelydrid taxa, in contrast to regularly occurring sympatric pan-trionychids, pan-testudinids or pan-geoemydids (Lapparent de Broin 2001). Therefore, it is apparent that European pan-chelydrids never fully speciated as a response to barriers, as fully formed species should have lived in sympatry in some regions, at least for a period of time, after the collapse of geographic barriers.

Chelydropsis decheni and *Chelydropsis sanctihenrici* are nearly coeval (MP 30 compared with MP 26, respectively), and both occur within the northern Alpine foreland basin; I here interpret all documented differences to be related to ontogeny. *Chelydropsis apellanizi* is somewhat younger (Neogene European Mammal Zone [MN] 3) and occurs south of the rising Pyrenees in northern Spain, but the material is insufficient to rigorously distinguish it from its northern counterparts. I therefore group all three taxa into a single taxon, *Chelydropsis decheni*.

Fraas (1870) initially referred pan-chelydrid material from the Middle Miocene of Steinheim (MN 7+8), Germany, to *Chelydropsis decheni*; however, Młynarski (1980b) transferred this material to the younger *Chelydropsis murchisoni*. I agree with that assessment. Młynarski (1963) similarly assigned fragmentary specimens from the Late Pliocene (MN 16) of Hajnáčka, Slovakia, to *Chelydropsis decheni* but later referred this material to *Chelydropsis pontica* (Młynarski 1980a, 1980b). However, given the fragmentary nature of these remains, these are better interpreted as *Chelydropsis* indet. (Danilov et al. 2012). Additional pan-chelydrid material has been described from Oligocene to Early Miocene localities throughout Europe (see Appendix 3), but this material lacks the diagnostic characteristics of *Chelydropsis decheni* and is therefore herein assigned to *Chelydropsis* indet.

Chelydropsis kusnetzovi Chkhikvadze in Gaiduchenko and Chkhikvadze, 1985

Taxonomic history. *Chelydropsis kusnetzovi* Chkhikvadze in Gaiduchenko and Chkhikvadze, 1985 (new species).

Type material. IPGAS 6-1-3 (holotype), a partial carapace preserved in dorsal view (Gaiduchenko and Chkhikvadze 1985, unnumbered figure).

Type locality. Locality of Detskaya zheleznaya doroga (= Gusinyy perelet = Pavlodar), Pavlodar Region, Kazakhstan (Figure 7); Koryakovskaya Svita (Formation), Early Pliocene (Gaiduchenko and Chkhikvadze 1985; Chkhikvadze 1987).

Referred material and range. Early Pliocene of Pavlodar Region (type locality), Kazakhstan (Gaiduchenko and Chkhikvadze 1985; Chkhikvadze 1987).

Diagnosis. *Chelydropsis kusnetzovi* can be diagnosed as a pan-chelydrid by the full list of shell characters given for that clade above. The placement of *Chelydropsis kusnetzovi* within *Chelydropsis* is here based purely on biogeographic considerations. *Chelydropsis kusnetzovi* is similar to the older *Chelydropsis decheni* in having a triangular anterior plastral lobe but differs from the coeval *Chelydropsis murchisoni* by lacking a rectangular anterior plastral lobe with broad epiplastra and a broad entoplastron.

Comments. In a series of papers, Chkhikvadze (1971, 1973, 1987) and Gaiduchenko and Chkhikvadze (1985) documented the presence of pan-chelydrids in Late Oligocene to Pliocene sediments in Kazakhstan and erected a total of three species: *Chelydropsis minax*, *Chelydropsis poena* and *Chelydropsis kusnetzovi*. The holotypes of the former two are isolated epiplastra (Chkhikvadze 1971), and subsequently referred rich material is insufficiently documented (Chkhikvadze 1973). I therefore dis-

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regarded these taxa as nomina dubia pending better description of the available material. In contrast to these two species, *Chelydropsis kusnetzovi* is based on a partial carapace, which, unfortunately, is only documented through a poorly executed illustration (Gaiduchenko and Chkhikvadze 1985) that cannot support a valid taxon either. However, Chkhikvadze (1987) soon after provided an unusually crisp photograph of a well-preserved, complete plastron. This specimen is interesting, as it has a narrow anterior plastral lobe, which replicates the symplesiomorphic morphology seen in *Chelydropsis decheni*, and not the wide anterior plastral lobe exhibited by coeval *Chelydropsis murchisoni*. It is therefore apparent that at least two plastral morphotypes were present in Eurasia during the Early Pliocene. I find this observation to be significant and therefore recognize the validity of *Chelydropsis kusnetzovi*. However, given how little material is described from Kazakhstan, I can only provide a meaningful diagnosis using a biogeographic rationale. It is therefore of utmost importance that the available material of *Chelydropsis kusnetzovi* be described in more detail.

Chelydropsis murchisoni (Bell, 1836) (= *Chelydra allingensis* Fuchs, 1939 = *Chelydropsis carinata* Peters, 1868 = *Chelydropsis murchisoni staeschei Młynarski*, 1980b = *Macrocephalochelys pontica* Pidoplichko and Tarashchuk, 1960 = *Trionyx sansaniensis* Bergounioux, 1935)

Taxonomic history. *Chelydra murchisoni* Bell, 1836 (new species); *Chelydropsis murchisoni* Broin, 1977 (new combination); *Chelydropsis murchisoni* = *Chelydra allingensis* Młynarski, 1980b (senior synonymy).

Type material. BMNH 37204 (holotype), a near-complete skeleton preserved in ventral view (Bell 1836, pl. 24; Lydekker 1889).

Type locality. Öhningen (= Oeningen or Oehningen), Baden-Württemberg, Germany (Figure 6); MN 7+8, Serravallian, Middle Miocene (Aguilar et al. 1997).

Referred material and range. Early to Middle Miocene (Aquitanian–Langhian) of Pyrenees Basin, France (hypodigm of *Chelydropsis sansaniensis* of Broin 1977 and Lapparent de Broin 2000); Middle Miocene (Serravallian) of Molasse Basin, including Öhningen (type locality), Germany (Meyer 1845, 1852; Winkler 1869; Fuchs 1939; Schleich 1981; Gaffney and Schleich 1994; Karl 2013); Middle Miocene (Burdigalian/Langhian) of Styria, Austria (type material of *Chelydropsis carinata*; Peters 1855, 1868, 1869); Middle to Late Miocene (Langhian–Messinian) of the Lower Rhine Embayment, Germany (Klein and Mörs 2003); Middle Miocene (Serravallian) of the Steinheim Basin, Germany (Fraas 1870; Młynarski 1980b); Middle Miocene (Serravallian) of Przeworno, Poland (Młynarski 1981a, 1981b); Late Miocene/Early Pliocene of Odessa Oblast/Province, Ukraine (Pidoplichko and Tarashchuk 1960; Tarashchuk 1971); Late Miocene/Early Pliocene of Crimea (Tarashchuk 1971).

Diagnosis. *Chelydropsis murchisoni* can be diagnosed as a representative of *Chelydropsis* by the full list of characters given above for this taxon. *Chelydropsis murchisoni* is currently differentiated from *Chelydropsis decheni* and *Chelydropsis kusnetzovi* by the presence of narrower peripherals, more pronounced serration to the posterior carapacial margin, a narrower bridge and a broad anterior plastral lobe with broad epiplastra and a broad entoplastron.

Comments. Fossil turtles were reported as early as the beginning of the 19th century from the locality of Öhningen (Karg 1805), but the available description of a turtle of the name "*Testudo orbicularis*" is too vague to allow determining whether a fossil pan-chelydrid was already known at that time. The locality of Öhningen is commonly reported incorrectly as being located in Switzerland (e.g., Lydekker 1889; Młynarski 1976; Broin 1977), but in fact is located within the current borders of Germany (Holy Roman Empire until 1806, Grand Duchy of Baden of the German Confederation until 1871), though within sight of Switzerland. I see three possibilities for this persisting error. First, among other important finds, the locality of Öhningen is probably most famous for having yielded the complete skeleton of a human that was introduced to the world as *homo diluvii testis* [man who witnessed the biblical deluge] by Scheuchzer (1726) in the book *Lithographia Helvetica*, a title that alludes to Switzerland. The specimen in question actually represents a giant cryptobranchid salamander (Holl 1831). Second, given the proximity of Öhningen to the Swiss border, much important work on this locality was undertaken by Swiss paleontologists (e.g., Heer 1847–1853, 1862) and may therefore have created the impression that Öhningen was located in that country. Finally, Meyer (1852) correctly, though confusingly, described Öhningen as being located "at the northern border of Switzerland."

Murchison (1832) reported a large turtle from Öhningen and noted that it reminded him of "*Testudo indica*." Bell (1832) concluded that the specimen was a fossil pan-chelydrid and soon after (Bell 1836) described and figured it under the name *Chelydra murchisoni*. A series of additional specimens of differing quality were later figured and described by Meyer (1845, 1852) and Winkler (1869). The holotype and at least two of the specimens figured by Winkler (1869) are now housed at the Natural History Museum in London (Lydekker 1889).

Broin (1977) presented good evidence to group all then-known pan-chelydrid material from Europe into two species groups, the Late Oligocene to Early Miocene *decheni*/*sanctihenrici* group and the Middle Miocene to Early Pliocene *murchisoni* group (also see *Chelydropsis decheni* above). Młynarski (1980a, 1980b) restricted the *murchisoni* group to the Middle Miocene and created the Late Miocene to Pliocene *pontica* group. I agree with Broin (1977) that many morphological differences exist between early and late representatives of European *Chelydropsis*, but material is currently insufficient to demonstrate the sequential acquisition of traits through time, although a general increase in size is apparent from the Late Oligocene to Late Pliocene. Given that not a single European locality has yielded two or more coeval pan-chelydrid species, I find it implausible to presume that European pan-chelydrids readily diversified into regional species but later never occurred in sympatry. I therefore presume that the European continent was inhabited by a single lineage that shows slow anagenetic change. As noted previously, Broin (1977) compiled sufficient morphological evidence to distinguish an early chronospecies

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(i.e., *Chelydropsis decheni*, her *decheni*/*sanctihenrici* group) from a late chronospecies (i.e., *Chelydropsis murchisoni*, her *murchisoni* group), but I find the Pliocene material too fragmentary to establish a third chronospecies as suggested by Młynarski (1980a, 1980b) (see Lapparent de Broin 2000 for a similar opinion). Given that the skull, anterior plastral lobe and posterior carapacial margin are the most diagnostic, I attribute all fossil material from Europe to *Chelydropsis decheni* and *Chelydropsis murchisoni* only if they preserve these anatomical regions. All remaining European material is referred to *Chelydropsis* indet. based on biogeographic considerations. Using these criteria, *Chelydropsis murchisoni* is known from material ranging from the Middle Miocene to Late Pliocene of France, Germany, Poland and Ukraine (see complete list of referred material above).

Chelydropsis murchisoni is known from well-preserved cranial material from multiple localities (e.g., Pidoplichko and Tarashchuk 1960; Tarashchuk 1971; Broin 1977; Młynarski 1981a, 1981b; Gaffney and Schleich 1994), which differs from extant pan-chelydrids by having broad triturating surfaces well adapted to crushing hard-shelled prey such as bivalves, crustaceans and gastropods. Although there is a strange tradition within the pan-chelydrid literature to not figure fossil specimens in palatal view (e.g., Tarashchuk 1971; Młynarski 1981a, 1981b; Erickson 2010), significant differences are nevertheless apparent in the relative size of triturating surfaces among material herein referred to *Chelydropsis murchisoni*, with specimens ranging from having relatively narrow (e.g., Gaffney and Schleich 1994) to extremely broad (e.g., undescribed material at MNHN) triturating surfaces. Although these differences could be used to support the validity of multiple species, I once again assign this to interspecific variation, as extant molluscivorous turtles often show a great amount of variation in the relative size of their palates due to ontogeny (e.g., the trionychid *Apalone ferox*; Dalrymple 1977) or sexual dimorphism (e.g., representatives of *Graptemys*; Lindeman 2003).

Denverus middletoni Hutchison and Holroyd, 2003

Taxonomic history. *Denverus middletoni* Hutchison and Holroyd, 2003 (new species).

Type material. UCM 48400 (holotype), a partial shell consisting, among other fragments, of eight partial costals, three neurals, a partial suprapygal, left peripherals VI–VIII, right peripheral VII, left hyoplastron and right hypoplastron (Hutchison and Holroyd 2003, figs. 8 and 9).

Type locality. UCM locality 79013, El Paso County, Colorado, USA (Figure 5); Denver Formation, Puercan NALMA (Hutchison and Holroyd 2003), Danian, Early Paleocene (Woodburne 2004).

Referred material and range. Early Paleocene (Danian), Puercan NALMA, Denver Formation, El Paso County, Colorado, USA (Hutchison and Holroyd 2003).

Diagnosis. *Denverus middletoni* can be tentatively diagnosed (see Comments below) as a pan-chelydrid by the presence of a reduced, cruciform plastron; lack of a midline contact of the abdominals; three or four contiguous inframarginals; and the presence of a surface sculpturing consisting of fine plications. Among pan-chelydrids, *D. middletoni* is differentiated from *Chelydropsis* spp. and *Protochelydra zangerli* by the greater anteroposterior width of the bridge, by being distinctly tricarinate, and by termination of the inguinal buttress on peripheral VII. *D. middletoni* is differentiated from crown chelydrids by absence of plastral fontanelles, presence of sockets in the peripherals for articulation with the plastron and more extensive buttresses.

Comments. *Denverus middletoni* is based on a partial shell from the Early Paleocene of Colorado. Although the available material is highly fragmentary, this taxon can readily be distinguished from other early pan-chelydrids by its small size and from pan-kinosternoids by the thin nature of its plastron. However, it is not possible to rigorously diagnose this taxon as a pan-chelydrid, as it universally displays symplesiomorphic characters of *Chelydroidea*. I here follow Holroyd and Hutchison (2002) and Holroyd et al. (2014) by diagnosing this taxon as a pan-chelydrid by the presence of a surface texture consisting of fine plications.

Protochelydra zangerli Erickson, 1973

Taxonomic history. *Protochelydra zangerli* Erickson, 1973 (new species).

Type material. SMM P72.34.20 (holotype), a partial skull primarily lacking much of the right facial region (Erickson 1973, figs. 1–3).

Type locality. Wannagan Creek Quarry, NW 1/4, Section 18, T141N, R102W, Billings County, North Dakota, USA (Erickson 1973; Figure 5); Tongue River Formation, Tiffanian 4 NALMA (Erickson 2010), Thanetian, Late Paleocene (Woodburne 2004).

Referred material and range. Late Paleocene (Danian–Selandian), type locality (Erickson 1973, 1982, 1984, 2010); Middle to Late Paleocene, Paskapoo Formation, southern Alberta (Brinkman 2013); Late Paleocene, Chickaloon Formation, Clarkforkian, Alaska (Hutchison and Pasch 2004).

Diagnosis. *Protochelydra zangerli* is diagnosed as a pan-chelydrid by the full list of characters provided for that clade above. Among pan-chelydrids, *P. zangerli* is differentiated from *Chelydropsis* spp. by the contribution of the jugal to the orbit and from *Denverus middletoni* in having a narrower bridge and lacking distinct carinae. *P. zangerli* is differentiated from chelydrids by absence of plastral fontanelles, presence of sockets in the peripherals for articulation with the plastron and more extensive buttresses.

Comments. The fossil locality of Wannagan Creek in North Dakota has yielded rich remains of the pan-chelydrid *Protochelydra zangerli*, including well-preserved cranial material (Erickson 1973, 1984, 2010), and its taxonomic validity is therefore uncontroversial. Fragmentary material has been referred to *P. zangerli* from the Campanian of Mexico (Rodriguez-de la Rosa and Cevallos-Ferriz 1998), the Maastrichtian of Montana and

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North Dakota (Holroyd and Hutchison 2002) and the Paleocene and Eocene of Wyoming (Bartels 1983; Holroyd et al. 2001); however, given that figured or detailed character analyses are lacking, I herein more carefully identify all of this material to *Pan-Chelydridae* indet. Well-preserved and well-figured material has been referred to this species from the Paleocene of Alaska (Hutchison and Pasch 2004) and Alberta (Brinkman 2013), and I agree with these taxonomic assessments. To allow future authors to more rigorously diagnose their material as belonging to *P. zangerli*, I urge the redescription of all available material from the type locality.

Chelydridae Swainson, 1839

Phylogenetic definition. Following Joyce et al. (2004), the name *Chelydridae* is herein referred to the clade arising from the last common ancestor of *Chelydra serpentina* (Linnaeus, 1758) and *Macrochelys temminckii* (Troost in Harlan, 1835).

Diagnosis. Representatives of *Chelydridae* are currently differentiated relative to more basal pan-chelydrids by the retention of costal and plastral fontanelles in skeletally mature individuals and by lacking pegs and sockets in the bridge.

Macrochelys Gray, 1856

Type species. *Macrochelys temminckii* (Troost in Harlan, 1835).

Diagnosis. *Macrochelys* can be diagnosed to be a representative of *Pan-Chelydridae* and *Chelydridae* by the full list of characters given for those clades above. *Macrochelys* can be distinguished from other chelydrids, notably *Chelydra serpentina*, by being strongly macrocephalic and having less well-developed upper and lower temporal emarginations, a reduced basisphenoid, a more strongly protruding processus trochlearis oticum, a broad nuchal notch, three rows of well-developed carapacial knobs, strong peripheral serrations, thickened peripherals, a more extensive bridge and a less developed epiplastral beak. The postcranial characters are currently only well known for *M. temminckii* and *M. auffenbergi*.

Macrochelys auffenbergi Dobie, 1968

Taxonomic history. *Macroclemys auffenbergi* Dobie, 1968 (new species); *Macrochelys auffenbergi* Hutchison, 2008 (new combination).

Type material. UF 10992 (holotype), a near-complete skeleton primarily lacking most of the skull (Dobie 1968, fig. 1a–c); UF 11053 (paratype), skull and mandible (Dobie 1968, fig. 1d); UF 9198, UF 9199 (paratypes), partial skulls (Dobie 1968, fig. 1d); UF 9242 (paratype), a partial shell; UF 9224–9228, UF 13051–13061 (paratypes), humeri (Dobie 1968, fig. 1b); UF 13062, UF 13063, UF 13064 (paratypes), proximal phalanges.

Type locality. McGehee Site, S ½, NW ¼, Section 22, T9S, R17E, Alachua County, Florida, USA (Dobie 1968; Figure 5); early Hemphillian NALMA (Thomas et al. 2014), Tortonian, Late Miocene (Thomas et al. 2014).

Referred material and range. No specimens have been referred to date beyond the paratypes listed above. Thomas et al. (2014) report the presence of additional material of *Macrochelys auffenbergi* but do not figure specimens or provide catalog numbers.

Diagnosis. *Macrochelys auffenbergi* can be diagnosed to be part of *Macrochelys* based on the full list of characters given above for that clade. *M. auffenbergi* can be differentiated from *M. schmidti* by the presence of narrower pterygoids, laterally oriented eyes and more strongly hooked jaws; from *M. stricta* by having less well-developed lingual ridges; and from *M. temminckii* by being less macrocephalic, having better developed lingual ridges and having narrower triturating surfaces.

Comments. The Late Miocene McGehee Site in Florida has yielded a rich collection of beautifully preserved pan-chelydrid material, including skulls, shells and limb bones, which serves as the basis for *Macrochelys auffenbergi*, and the validity of this species has therefore never been controversial. Thomas et al. (2014) highlighted systematic differences between *M. auffenbergi* and all recent populations of *Macrochelys*, and it is therefore reasonable to speculate that this species is the immediate sister to all extant *Macrochelys* (Whetstone 1978a).

Macrochelys schmidti Zangerl, 1945

Taxonomic history. *Macrochelys schmidti* Zangerl, 1945 (new species); *Macroclemys schmidti* Williams, 1952 (new combination).

Type material. FMNH P26014 (holotype), a nearly complete skull (Zangerl 1945, figs. 2 and 3).

Type locality. East Clayton Quarry, Marsland, Dawes County, Nebraska, USA (Figure 5); Marsland Formation, early Hemingfordian NALMA (Zangerl 1945), Burdigalian, Early Miocene (Woodburne 2004).

Referred material and range. Early Miocene, type formation, Butte County, Nebraska (Whetstone 1978a).

Diagnosis. *Macrochelys schmidti* can be diagnosed as part of *Macrochelys* by the full list of cranial characters given for that taxon above. *M. schmidti* can be differentiated from all remaining *Macrochelys* by the symplesiomorphic retention of relatively wide pterygoids, dorsoventrally oriented eyes, more elongate jugals and lacking strongly hooked jaws.

Comments. *Macrochelys schmidti* is based on a small (basioccipital to tip of snout: 72 mm), partially crushed skull from the Early Miocene of Nebraska (Zangerl 1945). Although Zangerl (1945) provided beautifully crafted stipple drawings of the type specimen, many anatomical details remain obscure. Whetstone (1978a) later referred a much larger and much better-preserved skull from the type formation of a neighboring county in Nebraska to this species, but a detailed description is missing for this well-preserved specimen as well. Much therefore remains unclear regarding the morphology of *M. schmidti*, and a revision is therefore long overdue. However, I agree in the list of systematic differences that Whetstone (1978a) provided to differentiate *M. schmidti* relative to other *Macrochelys* species.

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The species "*Macrochelys schmidti*" was recently included into the global phylogenies analysis of Sterli et al. (2013). The scoring is based on AMNH FAM11556, which is cataloged as a representative of that taxon. However, this specimen originates from the Middle to Late Miocene (Clarendonian NALMA) of Nebraska, not the Early Miocene (early Hemingfordian) of the same state; lacks the symplesiomorphic characteristics diagnostic of *M. schmidti*; and is therefore temporally and morphological much closer to *M. stricta* (see *Macrochelys stricta* below) but lacks the lingual ridges diagnostic of *M. stricta*. Although AMNH FAM11556 still demands formal description and evaluation, I nevertheless think it safe to assume that it does not represent *M. schmidti*.

Macrochelys stricta (Matthew, 1924)

Taxonomic history. *Chelydrops stricta* Matthew, 1924 (new species); *Macrochelys stricta* Hutchison, 2008 (new combination).

Type material. AMNH 6297 (holotype), a partial skull consisting mostly of the snout region (Matthew 1924, fig. 63).

Type locality. Snake Creek Beds, Sioux County, Nebraska, USA (Figure 5); Snake Creek Formation (Matthew 1924), Ogallala Group, Barstovian NALMA, Langhian–Serravallian, Middle Miocene (Woodburne 2004).

Referred material and range. No material has been referred to date.

Diagnosis. *Macrochelys stricta* can be diagnosed to be part of *Macrochelys* by being macrocephalic and lacking well-developed lower temporal emarginations. *M. stricta* can be differentiated from *M. schmidti* by the presence of narrower pterygoids, laterally oriented eyes and more strongly hooked jaws, and from *M. auffenbergi* and *M. temminckii* by exhibiting better-developed lingual ridges.

Comments. *Macrochelys stricta* is based on a partial skull consisting of the snout region of a large turtle from Nebraska and is intermediate in age between the Early Miocene *M. schmidti* and the Late Miocene *M. auffenbergi*. I agree with Hutchison (2008) that this species can be retained pending more detailed description and comparison with other taxa. The most compelling character that supports the validity of this species is the strong development of two lingual ridges.

Invalid and Problematic Taxa

Broilia robusta Bergounioux and Crouzel, 1965
nomen dubium

Taxonomic history. *Broilia robusta* Bergounioux and Crouzel, 1965 (new species); *Broila robusta* Bergounioux and Crouzel, 1965 (incorrect spelling); *Chelydropsis sansaniensis* = *Broilia robusta* (in part) = *Leptochelys braneti* Broin, 1977 (junior synonym); Hutchison, 2008 (lectotype designation).

Type material. MNHN SA uncat. (lectotype), a string of "caudal" vertebrae (Bergounioux and Crouzel 1965, fig. 6), a chimera composed of chelydrid caudals and mammalian cervicals (Broin 1977); MNHN SA uncat. (paralectotypes), elements from several specimens, including shell fragments and limb elements (Bergounioux and Crouzel 1965, figs. 10–15), a chimera composed of pan-chelydrid and pan-testudinid remains (Broin 1977; Hutchison 2008).

Type locality. Sansan, Department of Gers, France (Bergounioux and Crouzel 1965); MN 6, Langhian, Middle Miocene (Aguilar et al. 1997).

Comments. *Broilia robusta* is one of many taxonomic travesties created by Bergounioux (see *Leptochelys braneti* for another example). The species is typified based on an assemblage of specimens from the Miocene locality of Sansan, France (Bergounioux and Crouzel 1965), but later studies revealed this assemblage to be a chimera that includes pan-chelydrid, pan-testudinoid and mammalian material (Chkhikvadze 1971; Broin 1977; Hutchison 2008). Hutchison (2008) attempted to resolve this issue by designating the caudal series as the lectotype, but this only partially resolved the issue, as Broin (1977) already demonstrated the caudal series to include mammalian cervicals in addition to pan-chelydrid caudals.

At this point, two possibilities remain to achieve nomenclatural stability: (1) designate a mammalian cervical as the "lectolectotype," thereby rendering this taxon irrelevant to the evolution of chelydrids; or (2) designate a single pan-chelydrid caudal as the "lectolectotype," thereby creating yet another poorly diagnosed pan-chelydrid taxon. Given that material from Sansan has already been used to typify up to four (!) pan-chelydrid taxa (see *Emys sansaniensis Leptochelys braneti* and *Trionyx sansaniensis*), of which *Broilia robusta* would at best been shown to be a junior synonym, I see no need to further resolve the taxonomic validity of this taxon and treat it as a nomen dubium.

Chelydra allingensis Fuchs, 1939
nomen invalidum
(= *Chelydropsis murchisoni* [Bell, 1836])

Taxonomic history. *Chelydra allingensis* Fuchs, 1939 (new species); *Chelydra allinghensis* Williams, 1952 (incorrect spelling of species epithet); *Chelydropsis murchisoni* = *Chelydra allingensis* Młynarski, 1980b (junior synonymy); *Chelydropsis allingensis* Schleich, 1981 (new combination).

Type material. BSPG LI 118 (syntype), partial shell consisting of nuchal, two peripherals, two costals and a cervical vertebra; BSPG LI 128 (syntype), partial left carapace; BSPG LI 129 (syntype), right femur; BSPG LI 322 (syntype), right epiplastron; BSPG LI 592 (syntype), left partial hyoplastron in articulation with neighboring peripherals; BSPG LI 593 (syntype), partial skull? and girdle remains; BSPG LI 594 (syntype), six articulated costals and peripherals; BSPG LI 595 (syntype), articulated carapace fragments; BSPG LI 651 (syntype), our peripherals and shattered scapulacoracoid (parts figured in Fuchs 1939, fig. 26).

Type locality. Viehhausen, Bavaria, Germany; MN 5, Burdigalian/Langhian, Early/Middle Miocene (Aguilar et al. 1997).

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Comments. *Chelydra allingensis* is based on a collection of fragments retrieved from the Miocene locality of Viehhausen (Fuchs 1939). The syntype series was originally housed in the collections of the University of Würzburg but was recently transferred to BSPG. Given that the old numbering system does not correspond to the new numbering system, I here only provide the new BSPG numbers. Fuchs (1939) originally diagnosed this taxon relative to other chelydrids based on nuances to the proportions of the carapacial and plastral scutes, but I find the material, in particular the expanded epiplastron, to fully overlap in its morphology with *Chelydropsis murchisoni*, which is typified by only slightly older material from nearby Öhningen, Germany.

Chelydra argillarum Laube, 1900 nomen dubium

Taxonomic history. *Chelydra argillarum* Laube, 1900 (new species).

Type material. SNSD-MMG CsT 611 (holotype), poorly preserved partial skeleton of a juvenile on a single slab of rock (Laube 1900, pl. 3.3).

Type locality. Břešťany (= Preschen) near the town of Bílina (= Bilin), Ústecký Region, Czech Republic; MN 3, Burdigalian, Early Miocene (Aguilar et al. 1997).

Comments. *Chelydra argillarum* is based on a juvenile specimen recovered from sediments exposed in modern-day Czech Republic. As already indicated by Laube (1900), the type specimen was deposited in collections in Dresden, Germany, and I was able to confirm their current whereabouts at SNSD-MMG. Given that juvenile turtles, including this specimen, have poorly ossified shells, it is generally imprudent to use them to typify species. I therefore regard this taxon to be a nomen dubium.

Chelydra laticarinata Hay, 1916 nomen invalidum (junior synonym of *Chelydra serpentina* [Linnaeus, 1758])

Taxonomic history. *Chelydra laticarinata* Hay, 1916 (new species); *Chelydra osceola* = *Chelydra laticarinata* Richmond, 1958 (junior synonym); *Chelydra serpentina* = *Chelydra laticarinata* Weigel, 1962 (junior synonym).

Type material. USNM V8827 (holotype, formerly FGS 7094), an isolated left peripheral VI (Hay 1916, pl. 6.6, 7).

Type locality. Vero, Saint Lucie County, Florida, USA; Pleistocene (Hay 1916).

Comments. *Chelydra laticarinata* and *Chelydra sculpta* (see *Chelydra sculpta* below) are based on isolated peripherals that were found in poorly dated Pleistocene deposits in Florida. Weigel (1962) suggested that these taxa may be synonymous with *Chelydra serpentina*, but Richmond (1958) and Feuer (1971) more precisely suggested them to be synonymous with the extant Florida snapping turtle *Chelydra osceola* Stejneger, 1918. However, given that the names *laticarinata* and *sculpta* precede *osceola*, Smith et al. (1983) petitioned the International Commission on Zoological Nomenclature (ICZN) to suppress both in favor of *osceola*, a request soon after granted by the ICZN (1986). Given that *osceola* shows gradation toward the main population of *serpentina* farther to the north (e.g., Feuer 1971), this taxon is currently considered to be a subspecies of the latter. I therefore consider *laticarinata* and *sculpta* to be regular junior synonyms of *serpentina*, as otherwise suggested by Ernst (2008).

Chelydra sculpta Hay, 1916 nomen invalidum (junior synonym of *Chelydra serpentina* [Linnaeus, 1758])

Taxonomic history. *Chelydra sculpta* Hay, 1916 (new species); *Chelydra osceola* = *Chelydra sculpta* Richmond, 1958 (junior synonym); *Chelydra serpentina* = *Chelydra sculpta* Weigel, 1962 (junior synonym).

Type material. USNM V8826 (holotype, formerly FGS 5510), an isolated right peripheral IX (Hay 1916, pl. 6.8, 9).

Type locality. Vero, Saint Lucie County, Florida, USA; Pleistocene (Hay 1916).

Comments. See *Chelydra laticarinata* (above).

Chelydropsis apellanizi Murelaga et al., 1999 nomen invalidum (junior synonym of *Chelydropsis decheni* [Meyer, 1852])

Taxonomic history. *Chelydropsis apellanizi* Murelaga et al., 1999 (new species); *Chelydrasia apellanizi* Hutchison, 2008 (new combination).

Type material. UPV/EHU BF 58 (holotype), a left hyoplastron (Murelaga et al. 1999, fig. 2c, d); UPV/EHU BF 19, left peripheral X, UPV/EHU BF 20, right peripheral IX, UPV/EHU BF 21, pygal, UPV/EHU BF 23, neural I, UPV/EHU BF 64, right hypoplastron, UPV/EHU BF 74, neural, UPV/EHU BF 113, right xiphiplastron, UPV/EHU BF 131, partial left epiplastron (paratypes) (Murelaga et al. 1999, figs. 1a–j and 2a, e–h).

Type locality. Barranco del Fraile site, Bardenas Reales, Navarre, Spain; MN 3, Burdigalian, Early Miocene (Murelaga et al. 1999).

Comments. Early Miocene outcrops at the Barranco del Fraile site in northern Spain have yielded a total of 21 chelydrid fragments, which have served as the basis of *Chelydropsis apellanizi* (Murelaga et al. 1999; Murelaga et al. 2002). Although I agree that the taxon was attributed to the *decheni-sanctihenrici* group of Broin (1977), I am less convinced by its diagnosis as a distinct taxon, given that the proposed differences are more reasonably attributed to ontogenetic variation. For an extensive justification, see *Chelydropsis decheni* (above).

Together with material from Turkey (Paicheler et al. 1978), fossil pan-chelydrids from Spain are notable, as they are the only specimens known from south of the greater Alpine/Himalayan mountain chain that runs throughout Europe and Asia. At this point, however, I find this observation insufficient to diagnose a valid taxon using geographic considerations.

Chelydropsis carinata Peters, 1868
nomen invalidum
(= *Chelydropsis murchisoni* [Bell, 1836])

Taxonomic history. *Chelydropsis carinata* Peters, 1868 (new species); *Chelydropsis carinatus* Młynarski, 1976 (incorrect spelling of species epithet).

Type material. Unknown location (holotype), a relatively complete carapace (Peters 1869, pl. 1). See Comments below regarding whereabouts of holotype.

Type locality. Coal seam von Eibiswald, Steyeregg, or Wies, Styria, exactly locality not provided (Peters 1868, 1869); MN 5, Burdigalian/Langhian, Early/Middle Miocene (Aguilar et al. 1997).

Comments. Peters first described fossil turtle material from Styria, Austria, under the name *Chelydra* sp. (Peters 1855), then under the new name *Chelydropsis carinata* (Peters 1868); finally, he provided a beautiful figure of the well-preserved type specimen, which consists of a nearly complete, large carapace (Peters 1869). Peters (1868) primarily diagnosed his taxon relative to other then-known chelydrids by the presence of a horizontally split nuchal, a double row of marginals and well-defined neurals. Williams (1952) and Młynarski (1976) already noted that the split nuchal is a taphonomic artifact, and I agree with this assessment. Peters's (1869) beautiful figure of the holotype furthermore does not evidence the presence of supernumerary marginals, but rather deep plications that partially divide the bridge marginals. The general morphology of *Chelydropsis carinata*, including the well-defined neurals, otherwise overlaps fully with that of *Chelydropsis murchisoni*; therefore, I synonymize these taxa with confidence.

Peters (1868) was correct in noting for the first time that European fossil chelydrid material varied systematically from extant North American taxa, and he created a new genus name to accommodate this observation. However, because all subsequent authors thought the presence of two nuchals to be an essential characteristic of *Chelydropsis*, newly named European taxa were still routinely assigned to the North American *Chelydra* (Laube 1900; Fuchs 1939; Schmidt 1966). Not until Chkhikvadze (1971) were all Eurasian taxa united under the name *Chelydropsis*.

Peters (1868, 1869) reported that the holotype was housed in the private collections of Letocha in Vienna, but I cannot find any references to this specimen in the literature from a later time. This specimen was not listed in a recent review of Austrian turtle (Gemel and Rauscher 2000) or in the list of turtles held in Graz (Gross 2002). I was able to furthermore clarify that it is currently neither held at the Naturhistorisches Museum Wien (= Natural History Museum) nor at the Geologische Bundesanstalt (= Federal Geological Survey of Austria). The whereabouts of this specimen are therefore currently unknown.

Chelydropsis minax Chkhikvadze, 1971
nomen dubium

Taxonomic history. *Chelydropsis minax* Chkhikvadze, 1971 (new species); *Chelydrasia minax* = *Chelydrasia poena* Młynarski, 1976 (junior synonym); *Chelydrasia minax* Chkhikvadze, 1999 (new combination).

Type material. IPGAS Z-35-25 (holotype), an isolated right epiplastron (Chkhikvadze 1971, fig. 1a).

Type locality. Tayzhuzgen ("Cherepakhovoe pole"), Zaisan Basin, East Kazakhstan, Kazakhstan; Kustovskaya Svita (Formation), Lower Oligocene (Chkhikvadze 1971).

Comments. Chkhikvadze (1971) reported fossil turtle material from the Tertiary Zaisan Basin of eastern Kazakhstan, which included the first known chelydrid material from the Asian continent. Of this material, Chkhikvadze (1971) figured and described two isolated epiplastra from the Lower Oligocene and Late Miocene under the names *Chelydropsis minax* and *Chelydropsis poena*, respectively. In his review of the turtles of the Zaisan Basin, Chkhikvadze (1973) soon after referred up to 400 fragments to this species, of which he figured about a dozen, which unambiguously confirm the presence of pan-chelydrids at this locality but, in my opinion, added little to their anatomy. The most notable feature that is apparent from this material is the presence of narrow epiplastra, a symplesiomorphic feature found among all pan-chelydrids.

It is notable that central Asia was partially to fully separate from Europe throughout much of the early Tertiary, and it is implausible that much genetic exchange took place across the existing oceanic barriers (Popov et al. 2004). However, the presence of plausible biogeographic barriers is not sufficient to support the validity of a fossil taxon. I therefore consider *Chelydropsis minax* and *Chelydropsis poena* to be undiagnostic and await the description of more comprehensive collections.

Chelydropsis staeschei Młynarski, 1980b
nomen invalidum
(= *Chelydropsis murchisoni* [Bell, 1836])

Taxonomic history. *Chelydropsis murchisoni staeschei* Młynarski, 1980b (new subspecies).

Type material. SMNS 50142 (holotype), a partial skeleton, including broken skull, mandible, anterior cervical vertebrae, shell and long bones (Młynarski 1980b, figs. 8 and 11, pls. 2b, c and 3a, d).

Type locality. Steinheim, Baden-Württemberg, Germany (Młynarski 1980b); MN 7/8, Serravallian, Middle-Miocene (Aguilar et al. 1997).

Comments. Młynarski (1980b) provided a comprehensive description of *Chelydropsis murchisoni* material from the Steinheim meteorite basin in southern Germany and noted systematic differences with material from other localities that he

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utilized to create a new subspecies, *Chelydropsis murchisoni staeschei*, as opposed to *Chelydropsis murchisoni murchisoni* from the type locality of Öhningen, Germany. Following the rules of the ICZN (1999), a subspecies name is considered equivalent to a species name, and I am therefore obliged to list this taxon in this contribution. However, given that I see no utility of utilizing subspecies names, I herein simply consider *staeschei* to be synonymous with *murchisoni*.

Chelydropsis poena Chkhikvadze, 1971
nomen dubium

Taxonomic history. *Chelydropsis poena* Chkhikvadze, 1971 (new species); *Chelydrasia minax* = *Chelydrasia poena* Młynarski, 1976 (junior synonym); *Chelydrasia poena* Hutchison, 2008 (new combination).

Type material. IPGAS Z-61-1 (holotype), an isolated left epiplastron (Chkhikvadze 1971, fig. 1b).

Type locality. Ashutas ("Kaymanovaya cherepakha"), Zaisan Basin, East Kazakhstan, Kazakhstan; Zhamangorinskaya Svita (Formation), Late Miocene (Chkhikvadze 1971).

Comments. See *Chelydropsis minax* (above).

Chelydropsis sanctihenrici Broin, 1977
nomen invalidum
(junior synonym of *Chelydropsis decheni* [Meyer, 1852])

Taxonomic history. *Chelydropsis sanctihenrici* Broin, 1977 (new species); *Chelydrasia sanctihenrici* Chkhikvadze, 1999 (new combination).

Type material. UL1 92837 (holotype), partial carapace lacking most of the right peripheral series and the right distal costals (Broin 1977, fig. 37, pl. 35.3).

Type locality. Saint-Henri, Marseille, Department of Bouches-du-Rhône, France; MP 26, Chattian, Late Oligocene (Aguilar et al. 1997).

Comments. *Chelydropsis sanctihenrici* is based on a small assortment of specimens collected from Late Oligocene sediments near the city of Marseille, France. Broin (1977) provided an excellent description of this material, including detailed figures, and the morphology of this taxon is therefore well characterized. Although Broin (1977) noted great similarities between *Chelydropsis sanctihenrici* and *Chelydropsis decheni*, she nevertheless felt justified to name a new species based on differences in size, the extent of the bridge and the presence of sculpturing, characters she readily admitted to perhaps be related to ontogenetic differences, as *Chelydropsis decheni* is mostly known from small, perhaps juvenile skeletons. Given that the close temporal and spatial proximity of both taxa, I here interpret these minor differences as regular interspecific variation and consider *Chelydropsis sanctihenrici* to be a nomen invalidum (see *Chelydropsis decheni* above).

Chelydra strausi Schmidt, 1966
nomen dubium

Taxonomic history. *Chelydra strausi* Schmidt, 1966 (new species); *Chelydropsis* (formerly *Trionyx*) *nopcsai* = *Chelydra strausi* = *Macrocephalochelys pontica* = *Testudo grandis* Chkhikvadze, 1980 (junior synonym); *Chelydropsis* (formerly *Trionyx*) *nopcsai* = *Chelydra strausi* Karl et al., 2012 (junior synonym).

Type material. GPIG/GZG W05873a (holotype), near-complete juvenile specimen (Schmidt 1966, fig. 1; Karl et al. 2012, fig. 1c).

Type locality. Willershausen, Lower Saxony, Germany (Schmidt 1966); MN 16/17, Piacenzian/Gelasian, Plio/Pleistocene (Aguilar et al. 1997).

Comments. *Chelydra strausi* is based on a relatively complete skeleton of a hatchling pan-chelydrid with a total body length of approximately 70 mm. Considering its small size, the specimen is surprisingly well preserved; however, most of the bones are not yet ossified, and the specimen therefore displays only few osteological details. Although some previous authors attempted to synonymize this taxon with others (e.g., Chkhikvadze 1980; Karl et al. 2012), I find it futile to evaluate the taxonomic identity of juvenile turtles. I therefore regard this taxon to be a nomen dubium.

Emys sansaniensis Lartet, 1851
nomen dubium

Taxonomic history. *Emys sansaniensis* Lartet, 1851 (new species).

Type material. Unknown.

Locality. Sansan, Department of Gers, France (Lartet 1851; Figure 5); MN 6, Langhian, Middle Miocene (Aguilar et al. 1997).

Comments. Lartet (1851) named a total of six fossil turtle taxa in his pioneering study on the Miocene fauna of Sansan, France, but he did not explicitly list any specimens or provide illustrations, making it near impossible to fully reproduce his taxonomic assignments. The brief taxonomic descriptions of Lartet (1851) highlights that *Emys sansaniensis* was a large turtle reaching a carapace length of up to 45 cm. Given that pan-chelydrids are the only known turtles to reach this size at Sansan, Broin (1977) reasoned that *E. sansaniensis* may represent a pan-chelydrid, but she also stressed that this rationale is highly speculative and that this taxon should be removed from taxonomic consideration. I fully agree with this assessment.

Emysaurus meilheuratiae Pomel, 1846
nomen dubium

Taxonomic history. *Emysaurus meilheuratiae* Pomel, 1846 (new species); *Chelydra meilheuratiae* Maack, 1869 (new combination); *Chelydropsis meilheuratiae* Chkhikvadze, 1971 (new combination).

Type material. All original material, at least a partial plastron, has never been figured and has been reported lost (Broin 1977).

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Type locality. Saint-Gérand-le-Puy, Department of Allier, France; MN 2, Aquitanian, Early Miocene (Aguilar et al. 1997).

Comments. Pomel (1846) named *Emysaurus meilheuratiae* in two short sentences in his summary of the turtle fauna from Saint-Gérand-le-Puy, France. The material on which this taxon was based was never figured and now seems to be lost (Broin 1977). It is clear from context, however, that Pomel (1846) at least had access to a plastron and that he purposefully placed his new taxon in the extant genus *Emysaurus* Duméril and Bibron, 1835, a junior synonym of *Chelydra* Schweigger, 1812. Some authors have since presumed that Pomel (1846) indeed described a pan-chelydrid (e.g., Chkhikvadze 1971; Broin 1977), but I find this to be purely speculative. I therefore interpret this taxon as a nomen dubium. Broin (1977) reports definite pan-chelydrid material from the type locality of *E. meilheuratiae*, but I do not consider Pomel (1846) to be an appropriate citation for this record.

Hoplochelys caelata Hay, 1908a
nomen dubium

Taxonomic history. *Hoplochelys caelata* Hay, 1908a (new species); *Protochelydra caelata* Hutchison, 2008 (new combination).

Type material. USNM 5958 (holotype), left peripherals VII–IX, right peripherals VIII–X and fragmentary costals (Hay 1908a, figs. 1–3).

Type locality. Section 35, T6N, R15E, Sweet Grass County, Montana, USA; Fort Union Formation, Paleocene (Hay 1908a).

Comments. *Hoplochelys caelata* is based on a few shell fragments from Paleocene sediments exposed in Montana (Hay 1908a). I agree with Hutchison and Holroyd (2003) that the flat peripherals and crenulated texture of the costals are more typical of a pan-chelydrid, but I find these remains to be far too fragmentary to allow any rigorous comparison with other pan-chelydrids. I therefore disregard this taxon as a nomen dubium.

Hydraspis oeningensis Fitzinger, 1836
nomen nudum

Material. Not applicable.

Locality. Not applicable.

Comments. Fitzinger (1836) provided a new taxonomy of turtles in a Latin compendium that includes full synonymy lists and references, but he refrained from listing characters or discussing taxonomic decisions. Some fossil taxa are listed in this contribution, but no information is provided beyond the name itself. This list includes the taxon *Hydraspis oeningensis*, which may perhaps be an allusion to the unnamed chelydrid that Bell (1832) had reported just a few years earlier from Öhningen, Germany. Meyer (1852) and Maack (1869) attributed the name "*oeningensis*" to Bell (1832, 1836), and Lydekker (1889) and Kuhn (1964) assigned the name to Meyer (1845), but I cannot confirm these assertions. The name *H. oeningensis* is therefore fully attributable to Fitzinger (1836). The ICZN (1999) demands little of names published during the 18th and 19th centuries, but a taxon must as least be associated with a description, definition or an indication, which may include a reference to a publication that provides a description or definition. Given that Fitzinger (1836) does not satisfy any of these requirements, it is apparent that this name is a nomen nudum.

Leptochelys braneti Bergounioux and Crouzel, 1965
unavailable name

Material. MNHN SA2023 (holotype), a partial hyo/hypoplastron (Bergounioux and Crouzel 1965, fig. 5).

Locality. Sansan, Department of Gers, France (Bergounioux and Crouzel 1965; Figure 5); MN 6, Langhian, Middle Miocene (Aguilar et al. 1997).

Comments. *Leptochelys braneti* is emblematic of the taxonomic doublethink practiced by Bergounioux. This taxon is based on a partial hyo/hypoplastron that Bergounioux and Crouzel (1965) originally interpreted as representing a carettochelyid, but that Chkhikvadze (1971) soon after correctly recognized to be a pan-chelydrid. More strangely, however, Bergounioux and Crouzel (1965) had already noted in the type description that *L. braneti* is the junior synonym of *Trionyx sansaniensis* Bergounioux, 1935. They therefore created a taxon that they already believed to be invalid during the naming process. Following the ICZN (1999), a taxon that is not treated as valid in the type description cannot be considered available. Given that up to four names are based on material from Sansan (see *Broilia robusta*), of which *L. braneti* could at best be shown to be a junior synonym, removing this taxon from consideration has little effect on the overall taxonomy of the group.

Macrocephalochelys pontica Pidoplichko and Tarashchuk, 1960
nomen invalidum
(= *Chelydropsis murchisoni* [Bell, 1836])

Taxonomic history. *Macrocephalochelys pontica* Pidoplichko and Tarashchuk, 1960 (new species); *Chelydropsis* (formerly *Trionyx*) *nopcsai* = *Chelydra strausi* = *Macrocephalochelys pontica* = *Testudo grandis* Chkhikvadze, 1980 (junior synonym); *Chelydropsis pontica* Młynarski, 1980b (new combination).

Type material. IZASU 42-1 (holotype), the slight deformed right half of a skull (Pidoplichko and Tarashchuk 1960, figs. 1–4).

Type locality. Odessa, Odessa Oblast/Province, Ukraine; Messinian, Late Miocene (Pidoplichko and Tarashchuk 1960).

Comments. *Macrocephalochelys pontica* is based on a relatively well-preserved and well-figured right half of a skull from Late Miocene ("Pontian") sediments exposed in Odessa, western Ukraine (Pidoplichko and Tarashchuk 1960). Tarashchuk (1971) later referred an unfigured mandible from the type locality to the same taxon, as well as a beautifully preserved and well-figured skull, which had been collected in similarly dated

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sediments on the Crimean peninsula farther to the east along the Black Sea coast.

Chkhikvadze (1980) united all then-known Pliocene chelydrids from Europe into a single taxon. The list of synonyms includes the purported trionychid *Trionyx nopcsai* Szalai, 1934; the purported tortoise *Testudo grandis* Macarovici and Vancea, 1959 (see *Testudo grandis* below); and the chelydrids *Chelydra strausi* and *Macrocephalochelys pontica*. Given the priority of *nopcsai* over the other names, Chkhikvadze (1980) introduced the new combination *Chelydropsis nopcsai* for this assemblage of material, and Hutchison (2008) replicated this decision. However, given that the type material of *Trionyx nopcsai* includes unambiguous, though lost pan-trionychid shell fragments in addition to a partial, purported pan-chelydrid mandible, Farkas (1995) designated the jaw fragment as the lectotype of *Chelydropsis nopcsai*.

Whereas I agree that part of the original syntype series of *Testudo grandis* is pan-chelydrid in nature (see *Testudo grandis* below), I have come to disagree with the conclusion of Młynarski (1966) and subsequent authors that *Trionyx nopcsai* is a pan-chelydrid. The lectotype of this taxon is the symphysis of a fragmentary mandible. The skull and mandibles of pan-chelydrids are short, and their mandibles therefore have an obtuse angle at the symphysis (Gaffney 1972; Młynarski 1980b). By contrast, the skulls and mandibles of pan-trionychids are elongate, and their symphysis therefore exhibits an acute angle. The triturating surface at the symphysis is furthermore narrow in pan-chelydrids, but somewhat broadened in pan-trionychids. The lectotype of *Trionyx nopcsai* does not resemble a pan-chelydrid in both regards, and I therefore think the original identification as a pan-trionychid to be more reasonable. Given that I refer all diagnostic Pliocene pan-chelydrid material from Europe to *Chelydropsis murchisoni*, this conclusion has little effect on the taxonomy being presented here. However, if future authors decide to resurrect a Pliocene taxon, *Chelydropsis pontica* would be the correct name attribution.

Although some European chelydrids had previously been known from skulls (e.g., Meyer 1845, 1852), their morphology was only poorly known because they were typically preserved crushed and in rock slabs. The beautifully preserved skull of *Macrocephalochelys pontica* therefore provides much fuel regarding the phylogenetic position of this taxon. Pidoplichko and Tarashchuk (1960) presumed this taxon to be a platysternid because the skull is notably high and the jugal does not contribute to the posterior margin of the eye, characters otherwise associated with *Platysternon megacephalum*. This hypothesis was supported by the phylogenetic arrangement of Gaffney (1975b), which placed *M. pontica* as sister to *P. megacephalum*, deep within crown *Chelydridae*. Chkhikvadze (1971), by contrast, argued that *M. pontica* is a pan-chelydrid and that platysternids were not closely related with these at all. The latter conclusion is now universally accepted based on molecular (e.g., Parham et al. 2006) and morphological (e.g., Lambertz et al. 2010) data, and all similarities of *P. megacephalum* with pan-chelydrids should now be viewed as convergences.

Macrochelys floridana Hay, 1907
nomen invalidum
(junior synonym of *Chelydra serpentina*
[Linnaeus, 1758])

Taxonomic history. *Macrochelys floridana* Hay, 1907 (new species); *Macrochelys temminckii* = *Macrochelys floridana* Auffenberg, 1957 (junior synonym); *Chelydra floridana* Thomas et al., 2014 (new combination and lectotype designation).

Type material. USNM 16676 (lectotype), an isolated peripheral (Hay 1907, figs. 2 and 3; Hay 1908b, figs. 284 and 285); USNM 16674, 16675, 16677 (lectotypes), three isolated peripherals (Hay 1907, figs. 1 and 4; Hay 1908b, figs. 283 and 286)

Type locality. Hillsborough County, Florida, USA; Pleistocene (Hay 1907).

Comments. *Macrochelys floridana* was originally based on four isolated peripherals from poorly dated Pleistocene sediments in Hillsborough County, Florida (Hay 1907), but Thomas et al. (2014) recently designated one of these four elements as the lectotype for this taxon, as they felt it to display the most diagnostic features. Auffenberg (1957) synonymized *M. floridana* with *M. temminckii* but did not provide an explicit rationale for this synonymy, although he did state that he used for comparison significant fossil and extant skeletal material held at UF. Thomas et al. (2014) more recently cited similar specimens at UF as evidence that *M. floridana* actually represents a valid taxon of giant common snapping turtle and suggested the new combination *Chelydra floridana*. However, it is not possible to reproduce this claim as none of the relevant material is figured or described.

I have since been able to view much of the relevant material at UF and agree with Thomas et al. (2014) that *Macrochelys floridana* indeed is referable to *Chelydra*, as the beautifully preserved skeletons closely correspond in their morphology to extant *Chelydra serpentina*. It is a matter of taxonomic preference, however, whether this material is viewed as a distinct species or as an enlarged Pleistocene form of the extant Florida snapping turtle *Chelydra serpentina osceola*. Given that I prefer naming lineage herein, I synonymize *M. floridana* with *Chelydra serpentina* but otherwise urge the description of the important material mentioned previously.

Testudo grandis Macarovici and Vancea, 1959
nomen dubium

Taxonomic history. *Testudo grandis* Macarovici and Vancea, 1959 (new species); *Chelydropsis* (formerly *Trionyx*) *nopcsai* = *Chelydra strausi* = *Macrocephalochelys pontica* = *Testudo grandis* Chkhikvadze, 1980 (junior synonym).

Type material. GIUI uncat. (lectotype), a peripheral (Macarovici and Vancea 1959, pl. 1.12); GIUI uncat. (paralectotypes), three shell fragments (Macarovici and Vancea 1959, pl. 2.7–9).

Type locality. Măluşteni, Vaslui County, Romania (Macarovici and Vancea 1959); MN 15, Zanclean, Early Pliocene (Aguilar et al. 1997).

Comments. *Testudo grandis* was originally described based on at least four figured turtle shell fragments from the Pliocene of eastern Romania (Macarovici and Vancea 1959). Młynarski (1969) soon after noted that the material consists of a mixture of pan-testudinid and pan-chelydrid remains. Chkhikvadze (1980)

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agreed with this assessment and therefore synonymized *T. grandis* with other Pliocene pan-chelydrids to form his comprehensive taxon *Chelydropsis nopcsai* (see *Macrocephalochelys pontica* above). Given that I find it undesirable to have chimeric type series, I herein designate as the lectotype of "*T.*" *grandis* the large peripheral fragment that Młynarski (1969) correctly identified as a pan-chelydrid. However, given that a single peripheral is not sufficient to diagnose a turtle taxon, I here additionally consider "*T.*" *grandis* to be a nomen dubium.

Trionyx sansaniensis Bergounioux, 1935
nomen invalidum
(= *Chelydropsis murchisoni* [Bell, 1836])

Taxonomic history. *Trionyx sansaniensis* Bergounioux, 1935 (new species); *Chelydropsis sansaniensis* Broin, 1977 (new combination).

Type material. MHNT SAN1163 (holotype), fragmentary right hyo/hypoplastron (Lapparent de Broin 2000, fig. 1).

Type locality. Sansan, Department of Gers, France (Bergounioux 1935); MN 6, Langhian, Middle Miocene (Aguilar et al. 1997).

Comments. The Miocene locality of Sansan in southwestern France has a long history of research. Lartet (1851) initially reported six species of fossil turtles from this locality, but given that he did not provide figures or specimen numbers most, if not all, of these should be considered nomen dubia (see *Emys sansaniensis* above). In his review of the fossil turtles of the Aquitaine Basin, Bergounioux (1935) recognized Lartet's taxa but nevertheless established yet another, *Trionyx sansaniensis*. The holotype, a partial right hyo/hypoplastron, was first presumed to be lost (Broin 1977) but could later be relocated and figured (Lapparent de Broin 2000). Broin (1977) already noted the pan-chelydrid nature of this taxon and therefore proposed the new combination *Chelydropsis sansaniensis*.

Under normal circumstances, the holotype of *Chelydropsis sansaniensis* should be considered undiagnostic, but the accumulative turtle material found at Sansan provides deep insights into the morphology of this pan-chelydrid (Broin 1977, Lapparent de Broin 2000). Broin (1977) already noted great similarities of the *Chelydropsis sansaniensis* with *Chelydropsis murchisoni*, but she nevertheless maintained the validity of this taxon, particularly based on nuances to the shape of the plastral bones. Following the rationale I developed herein (see *Chelydropsis murchisoni* above), I interpret these observations as interspecific variation and synonymize *Chelydropsis sansaniensis* with the nearly coeval type material of *Chelydropsis murchisoni*.

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Appendix 1
Institutional Abbreviations

AMNH	American Museum of Natural History, New York, New York, USA
BMNH	Natural History Museum, London, United Kingdom
BSPG	Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany
FGS	Geological Survey of Florida, collections now at UF or USNM
FMNH	Field Museum of Natural History, Chicago, Illinois, USA
GIUI	Geological Institut of the University of Iaşi, Iaşi, Romania
GPIG/GZG	Geowissenschaftliches Museum der Universität Göttingen, Göttingen, Germany
IPB	Steinmann-Institut für Geologie, Mineralogie und Paläontologie, Universität Bonn, Bonn, Germany
IPGAS	Institute for Paleobiology of the Georgian Academy of Sciences, Tbilisi, Georgia
IZASU	Institute of Zoology of the Academy of Sciences of Ukraine, Kiev, Ukraine
KU	University of Kansas Natural History Museum, Lawrence, Kansas, USA
MHNT	Muséum d'histoire naturelle de Toulouse, Toulouse, France
MNHN	Muséum national d'Histoire naturelle, Paris, France
NMW	Naturhistorisches Museum Wien, Vienna, Austria
SMM	Science Museum of Minnesota, St. Paul, Minnesota, USA
SMNS	Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany

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SNSD-MMG	Paläozoologische Sammlungen der Senckenberg Naturhistorischen Sammlungen Dresden, Museum für Mineralogie und Geologie, Dresden, Germany
UCM	University of Colorado Museum of Natural History, Boulder, Colorado, USA
UCMP	University of California Museum of Paleontology, Berkeley, California, USA
UF	Florida Museum of Natural History, Gainesville, Florida, USA
UL1	Collection du Laboratoire de Geologie, University of Lyon 1, Lyon, France
UPV/EHU	Universidad del Pais Vasco/Euskal Herriko Unibertsitatea, Bilbao, Spain
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington DC, USA

Appendix 2
Named Fossil Pan-Chelydrid Genera

Chelydrasia Chkhikvadze, 1999 (type species: *Chelydropsis minax* Chkhikvadze, 1971)

Chelydrops Matthew, 1924 (type species: *Chelydrops stricta* Matthew, 1924)

Chelydropsis Peters, 1868 (type species: *Chelydropsis carinata* Peters, 1868)

Denverus Hutchison and Holroyd, 2003 (type species: *Denverus middletoni* Hutchison and Holroyd, 2003)

Protochelydra Erickson, 1973 (type species: *Protochelydra zangerli* Erickson, 1973)

Appendix 3
Biogeographic Summary of Fossil *Pan-Chelydridae*

Numbers in brackets reference Figures 5–7. Holocene records and literature lacking vouched specimens are omitted. *Abbreviations*: MN, Neogene European Mammal Zone; MP, Paleogene European Mammal Zone; NALMA, North American Land Mammal Age; TL, type locality.

Austria

[1] Middle Miocene, Burdigalian/Langhian, MN 5; Eibiswald, Gratkorn, Steyeregg, Wies, Styria; *Chelydropsis murchisoni* (*Chelydropsis carinata* of Peters 1855, 1868, 1869; Gross 2002; Böhme and Vasilyan 2014)

Canada

[2] Late Cretaceous, Santonian; Alberta; *Pan-Chelydridae* indet. (*Chelydridae* indet. of Brinkman 2003)

[3] Late Cretaceous, Campanian; Alberta; *Pan-Chelydridae* indet. (*Chelydridae* indet. of Brinkman 2003; Brinkman and Eberth 2006)

[4] Late Cretaceous, Maastrichtian; Alberta; *Pan-Chelydridae* indet. (*Chelydridae* indet. of Brinkman 2003; Brinkman and Eberth 2006)

[5] Middle to Late Paleocene; vicinity of Calgary, Alberta; *Protochelydra zangerli* (Brinkman 2013)

[6] Middle to Late Paleocene; vicinity of Edmonton, Alberta; *Protochelydra zangerli* (Brinkman 2013)

Czech Republic

[7] Early Miocene, Burdigalian, MN 3; Břeštany (= Preschen) and Skyrice (= Skiritz), Ústecký Region; *Chelydropsis* indet. (*Chelydra argillarum* of Laube 1900; *Chelydra* sp. of Schlosser and Hibsch 1902; *Chelydra murchisoni* of Laube 1910)

France (see Broin 1977 for greater detail)

[8] Late Oligocene, Chattian, MP 28/29; Departments of Tarn-et-Garonne 9 and Lot-et-Garonne, Aquitaine Basin; *Chelydropsis* indet. (Broin 1977)

[9] Late Oligocene, Chattian, MP 25/26; Departments of Bouches-du-Rhône and Alpes-de-Haute-Provence, Rhone Basin; *Chelydropsis decheni* (*Chelydropsis sanctihenrici* of Broin 1977)

[10] Late Oligocene/Early Miocene, Chattian–Burdigalian, MP 29–MN 3; Departments of Allier, Puy-de-Dome, Upper Loire Valley; *Chelydropsis* indet. (Broin 1977)

[11] Early Miocene, Burdigalian, MN 3–4; Departments of Indre-et-Loire, Loiret, Loir-et-Cher, Maine-et-Loire, Paris Basin; *Chelydropsis* indet. (Broin 1977)

[12] Early to Middle Miocene, Aquitanian–Langhian, MN 1–6; Departments of Aude, Gers, Haute-Garonne, including Sansan (MN 6), Pyrenees Basin; *Chelydropsis* indet. (Broin 1977), *Chelydropsis murchisoni* (*Chelydropsis sansaniensis* of Broin 1977; Lapparent de Broin 2000; including *Broilia denticulata* of Bergounioux and Crouzel 1965 [in part]; *Broilia robusta* of Bergounioux and Crouzel 1965 [in part]; *Leptochelys braneti* of Bergounioux and Crouzel 1965; and *Trionyx sansaniensis* of Bergounioux 1935)

[13] Pliocene; Department of Pyrénées-Orientales; *Chelydropsis* indet. (*Chelydridae* indet. of Aymar 1992)

Germany

[14] Late Oligocene, Chattian, MP 30; North Rhine-Westphalia, Lower Rhine Embayment; *Chelydra decheni* (TL) (Meyer 1852, 1854, 1865)

[15] Oligocene, Chattian; Oberleiterbach, Bavaria, fissure fill; *Chelydropsis* indet. (Karl et al. 2011)

[16] Middle to Late Miocene, Langhian–Messinian, MN 5–13; North-Rhine-Westphalia, Lower Rhine Embayment; *Chelydropsis* indet. (Strauch 1990), *Chelydropsis murchisoni* (Klein and Mörs 2003)

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[17] Middle Miocene, Burdigalian/Langhian, MN 5; Appertshofen, Bavaria, fissure fill; *Chelydropsis* indet. (Groessens-Van Dyck and Schleich 1985)

[18] Middle Miocene, Serravallian, MN 7/8; Baden-Württemberg, Steinheim Basin; *Chelydra murchisoni* (Fraas 1870; Młynarski 1980b)

[19] Middle Miocene, Serravallian, MN 7/8; Baden Württemberg and Bavaria, Molasse Basin; *Chelydropsis* indet. (Karl 2013), *Chelydra murchisoni* (TL) (Bell 1836; Meyer 1845, 1852; Winkler 1869; Fuchs 1939; Schleich 1981; Gaffney and Schleich 1994)

[20] Late Miocene, Tortonian, MN 9; Baden-Württemberg, Höwenegg Marr Lake; *Chelydropsis* indet. (Schleich 1986)

Kazakhstan

[21] Early Oligocene; East Kazakhstan, Zaisan Basin; *Chelydropsis* indet. (*Chelydropsis minax* of Chkhikvadze 1971, 1973)

[22] Late Miocene; East Kazakhstan, Zaisan Basin; *Chelydropsis* indet. (*Chelydropsis poena* of Chkhikvadze 1971, 1973)

[23] Pliocene; North Kazakhstan, Ishim River; *Chelydropsis* indet. (*Testudo* sp. of Khosatzky 1944; *Chelydra* sp. of Khosatzky 1967, 1982; *Chelydropsis kusnetzovi* of Gaiduchenko and Chkhikvadze 1985)

[24] Pliocene; Pavlodar Province; *Chelydropsis kusnetzovi* (Gaiduchenko and Chkhikvadze 1985; Chkhikvadze 1987)

Mexico

[25] Late Cretaceous, Campanian; Coahuila; *Pan-Chelydridae* indet. (*Protochelydra* indet. of Rodriguez-de la Rosa and Cevallos-Ferriz 1998)

Moldova

[26] Middle Miocene; Buzhory, Hînceşti District; *Chelydropsis* indet. (*Chelydropsis murchisoni* of Khosatzky and Redkozubov 1989)

[27] Pliocene; Luceşti (= Lucheshty), Cahul District and Etulia, Gagaúzia District; *Chelydropsis* indet. (*Macrocephalochelys pontica* of Khosatzky and Redkozubov 1986; *Chelydropsis nopcsai* of Khosatzky and Redkozubov 1989)

Poland

[28] Middle Miocene, Serravallian, MN 7/8; Przeworno, Lower Silesian Voivodeship; *Chelydropsis murchisoni* (Młynarski 1981a, 1981b)

Romania

[29] Late Miocene, Tortonian, MN 9; Brusturi (= Tataros), Bihor (= Bihar) County; *Chelydropsis* indet. (*Chelydra* sp. of Młynarski 1966)

[30] Early Pliocene, Zanclean, MN 15; Măluşteni, Vaslui County; *Chelydropsis* indet. (part of *Testudo grandis* of Macarovici and Vancea 1959; *Chelydridae* indet. of Młynarski 1969)

Slovakia

[31] Late Pliocene, Piacenzian, MN 16; Hajnáčka, Banská Bystrica Region; *Chelydropsis* indet. (*Chelydra decheni* of Młynarski 1963; Danilov et al. 2012)

Spain

[32] Early Miocene, Burdigalian, MN 3; Bardenas Reales, Navarre; *Chelydropsis decheni* (*Chelydropsis apellanizi* of Murelaga et al. 1999; Murelaga et al. 2002)

[33] Late Pliocene, MN 15/16; Camp dels Ninots, Catalonia; *Chelydropsis* indet. (*Chelydropsis pontica* of Claude et al. 2014)

Ukraine

[34] Late Miocene/Early Pliocene; Odessa and Kuchurhan (= Kuchurgan), Odessa Oblast/Province; *Chelydropsis* indet. (*Testudo* sp. of Khosatzky 1949; *Chelydra* sp. of Khosatzky 1966, 1982; *Chelydropsis nopcsai* of Chkhikvadze 1980, 1982), *Chelydropsis murchisoni* (*Macrocephalochelys pontica* of Pidoplichko and Tarashchuk 1960; Tarashchuk 1971)

[35] Late Miocene/Early Pliocene; Crimea; *Chelydropsis murchisoni* (*Macrocephalochelys pontica* of Tarashchuk 1971)

Turkey

[36] Early to Middle Miocene; Beşkonak (= Bes-Konak), Ankara Province; *Chelydropsis* indet. (Paicheler et al. 1978)

United States of America

[37] Late Cretaceous, Campanian; Utah; *Pan-Chelydridae* indet. (*Chelydridae* indet. of Hutchison et al. 2013)

[38] Late Cretaceous, Maastrichtian; Montana; *Pan-Chelydridae* indet. (*Chelydridae* indet. of Holroyd and Hutchison 2002; Holroyd et al. 2014)

[39] Late Cretaceous, Maastrichtian; North Dakota; *Pan-Chelydridae* indet. (*Chelydridae* indet. of Holroyd and Hutchison 2002)

[40] Late Cretaceous, Maastrichtian; Wyoming; *Pan-Chelydridae* indet. (*Chelydridae* indet. of Holroyd and Hutchison 2002)

[41] Early Paleocene, Puercan NALMA, Danian; Montana; *Pan-Chelydridae* indet. (*Chelydridae* indet. of Hutchison and Archibald 1986; Holroyd and Hutchison 2002; Holroyd et al. 2014)

[42] Early Paleocene, Puercan NALMA, Danian; Colorado; *Denverus middletoni* (TL) (Hutchison and Holroyd 2003)

[43] Middle Paleocene, Torrejonian–Tiffanian NALMAs; Montana; *Pan-Chelydridae* indet. (*Hoplochelys caelata* of Hay 1908a)

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[44] Late Paleocene, Clarkforkian NALMA, Thanetian; Alaska; *Protochelydra zangerli* (Hutchison and Pasch 2004)

[45] Late Paleocene, Tiffanian NALMA, Selandian–Thanetian; North Dakota; *Protochelydra zangerli* (TL) (Erickson 1973, 1982, 1984, 2010)

[46] Late Paleocene, Clarkforkian NALMA, Thanetian; Wyoming; *Pan-Chelydridae* indet. (*Protochelydra zangerli* of Bartels 1983)

[47] Early Eocene, Wasatchian NALMA, Ypresian; Wyoming; *Pan-Chelydridae* indet. (*Chelydridae* indet. of Holroyd et al. 2001)

[48] Middle Eocene, Duchesnean NALMA, Bartonian; Oregon; *Pan-Chelydridae* indet. (*Chelydridae* indet. of Hanson 1996)

[49] Early Miocene, early Hemingfordian NALMA, Burdigalian; Nebraska; *Macrochelys schmidti* (TL) (Zangerl 1945; Whetstone 1978a)

[50] Middle Miocene, early Barstovian NALMA, Langhian; Nebraska; *Macrochelys stricta* (TL) (Matthew 1924), *Chelydridae* indet. (*Chelydra* sp. of Holman and Sullivan 1981; *Macrochelys* indet. of Holman and Corner 1985)

[51] Middle Miocene, early Barstovian NALMA, Langhian; Florida; *Macrochelys* indet. (Thomas et al. 2014)

[52] Late Miocene, Clarendonian NALMA, Serravallian/Tortonian; South Dakota; *Macrochelys* indet. (*Macrochelys temminckii* of Zangerl 1945)

[53] Late Miocene, late Clarendonian NALMA, Tortonian; Florida; *Chelydridae* indet. (Bourque 2013)

[54] Late Miocene, early Hemphillian NALMA, Tortonian; Florida; *Macrochelys auffenbergi* (TL) (Dobie 1968)

[55] Late Miocene/Early Pliocene, late Hemphillian NALMA, Messinian/Zanclean; Tennessee; *Chelydridae* indet. (*Chelydra serpentina* of Bentley et al. 2011)

[56] Late Miocene/Early Pliocene, late Hemphillian NALMA, Messinian/Zanclean; Florida; *Chelydridae* indet., *Macrochelys* indet. (Thomas et al. 2014)

[57] Pliocene, Blancan NALMA; northwestern Kansas; *Chelydra* indet. (Galbreath 1948; *Cheloniidae* indet. of Hibbard 1934, 1939)

[58] Pliocene, Blancan NALMA; southwestern Kansas; *Macroclemys* sp., *Chelydra indet.* (*Macroclemys temminckii* and *Chelydra serpentina* of Hibbard 1963)

[59] Pleistocene; Idaho; *Chelydra indet.* (Pinsof 1998)

[60] Pleistocene; Nevada; *Chelydra indet.* (Van Devender and Tessmann 1975)

[61] Pleistocene; northwestern Nebraska; *Chelydra indet.* (Preston 1979)

[62] Pleistocene; south central Nebraska; *Chelydra indet.* (Preston 1979)

[63] Pleistocene; central Kansas; *Chelydra indet.* (Holman 1972; Preston 1979)

[64] Pleistocene; southwestern Kansas; *Chelydra indet.* (Galbreath 1948; Hibbard and Taylor 1960; Schultz 1965; Preston 1971, 1979)

[65] Pleistocene; Oklahoma; *Chelydra* indet. (Preston 1979)

[66] Pleistocene; northern Texas; *Chelydra* indet. (Holman 1964)

[67] Pleistocene; central Texas; *Macrochelys* indet. (*Macrochelys temminckii* of Hay 1911)

[68] Pleistocene; Missouri; *Chelydra* indet. (Parmalee and Oesch 1972)

[69] Pleistocene; Illinois; *Chelydra* indet. (Holman 1966)

[70] Pleistocene; Michigan; *Chelydra* indet. (Wilson 1967)

[71] Pleistocene; Ohio; *Chelydra indet.* (Holman 1986)

[72] Pleistocene; Maryland; *Chelydra indet.* (Cope 1871; Hay 1908b)

[73] Pleistocene; South Carolina; *Chelydra indet.* (Dobie and Jackson 1979)

[74] Pleistocene; northern Florida; *Macroclemys* sp., *Chelydra serpentina* (*Chelydra floridana* of Thomas et al. 2014)

[75] Pleistocene; central Florida; *Macroclemys* sp., *Chelydra serpentina* (*Macrochelys floridana* of Hay 1907; *Chelydra laticarinata* and *Chelydra sculpta* of Hay 1916; *Macrochelys temminckii* of Auffenberg 1957; *Chelydra serpentina* of Meylan 1995; *Chelydra floridana* of Thomas et al. 2014)

Appendix 4
Hierarchical Taxonomy of Fossil *Pan-Chelydridae*

Pan-Chelydridae Joyce et al., 2004
  Chelydropsis Peters, 1868
    Chelydropsis decheni (Meyer, 1852)
    Chelydropsis kusnetzovi Chkhikvadze in Gaiduchenko and Chkhikvadze, 1985
    Chelydropsis murchisoni (Bell, 1836)
  Denverus middletoni Hutchison and Holroyd, 2003
  Protochelydra zangerli Erickson, 1973
    Chelydridae Swainson, 1839
      Macrochelys auffenbergi Dobie, 1968
      Macrochelys schmidti Zangerl, 1945
      Macrochelys stricta (Matthew, 1924)

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